

Quantifying Rearrangements in Pangenomes

Leonard Bohnenkämper

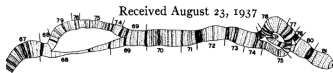
Bielefeld University

May 15th, 2025

Rearrangements

INVERSIONS IN THE CHROMOSOMES OF DROSOPHILA PSEUDOOBSCURA*

TH. DOBZHANSKY AND A. H. STURTEVANT
California Institute of Technology, Pasadena, California



INDEPENDENT FUNCTIONS OF VIRAL PROTEIN AND NUCLEIC ACID IN GROWTH OF BACTERIOPHAGE*

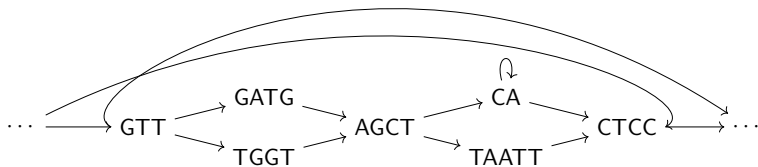
BY A. D. HERSHEY AND MARTHA CHASE

*(From the Department of Genetics, Carnegie Institution of Washington, Cold Spring
Harbor, Long Island)*

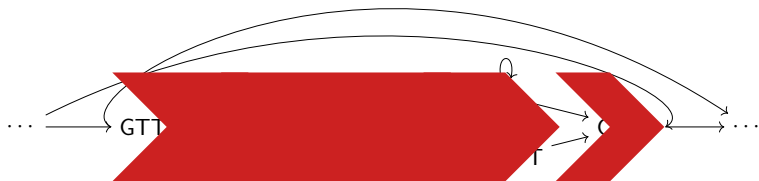
(Received for publication, April 9, 1952)

- ▶ ~30,000 inversions affect more bases of the human genome than ~5,000,000 SNVs
- ▶ Pivotal role in:
 - ▶ Evolution
 - ▶ Disease
- ▶ Rearrangement Quantification for Structural Variants \approx Alignment for SNVs

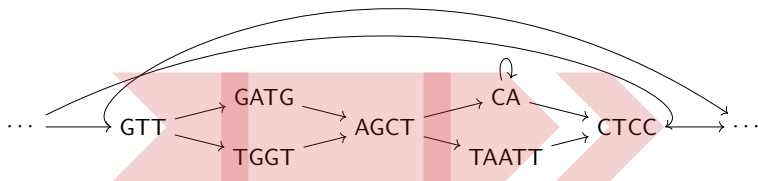
Abstracting from Local Variations



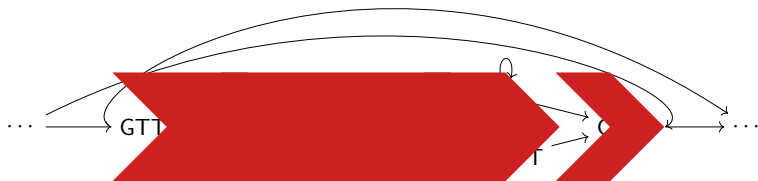
Abstracting from Local Variations



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→ Collinear Block Detection.

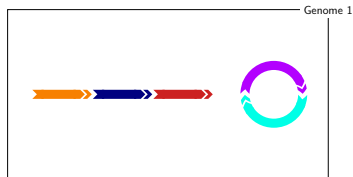
Marker, Chromosome, Genome, Pangenome



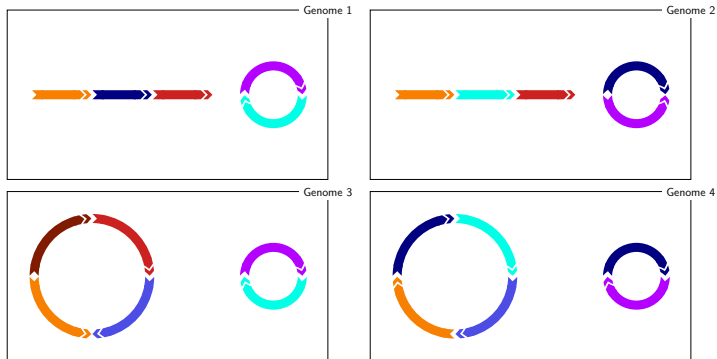
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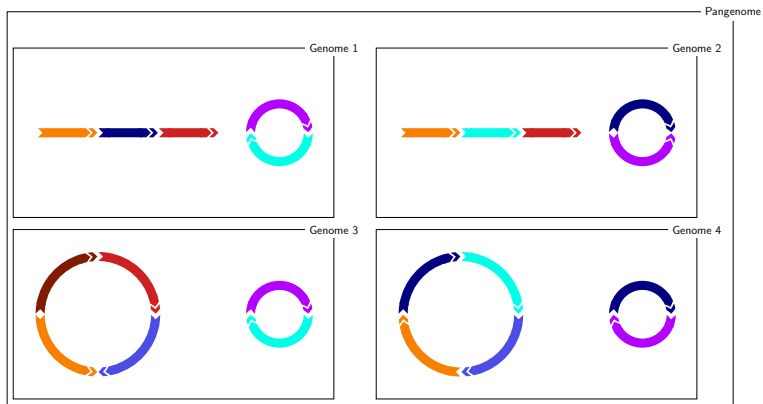
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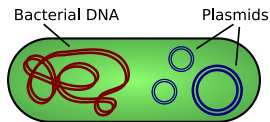


SPP - Ancestral Reconstruction with a Given Tree

Joint work with Daria Frolova (, Jens Stoye, Daniel Doerr)

Background: Plasmids

- ▶ Extrachromosomal DNA
- ▶ Common in bacteria
- ▶ Mostly circular
- ▶ Some plasmids can be transferred between hosts (even cross-species)
- ▶ Often carry resistance or virulence genes
- ▶ Frequent structural changes



Plasmid image by en: User:Spaully on English wikipedia, CC BY-SA 2.5, via Wikimedia Commons

Application: Plasmids

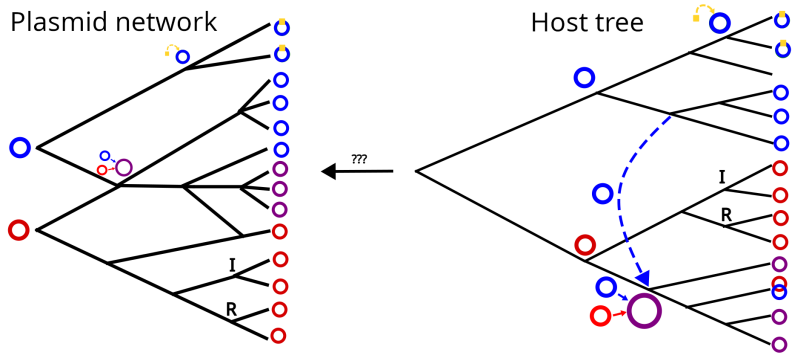


Image by courtesy of Daria Frolova

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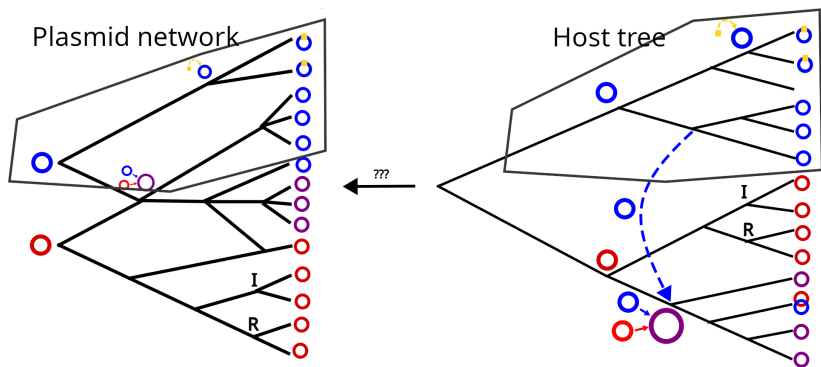
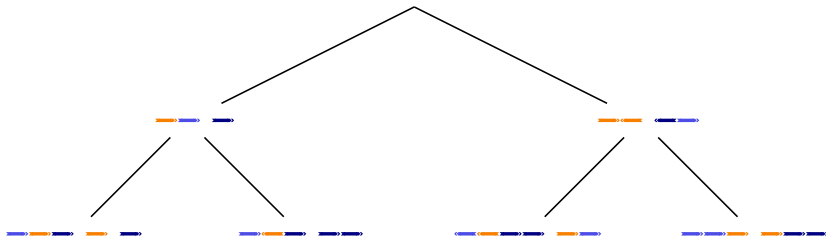
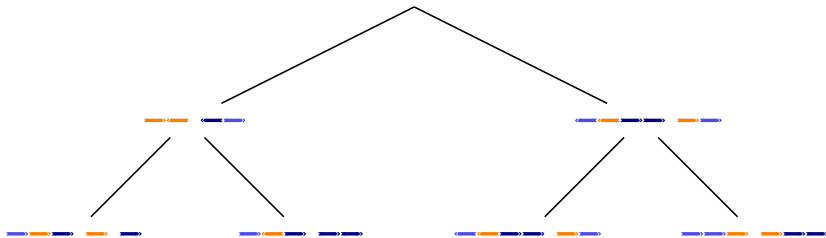


Image by courtesy of Daria Frolova

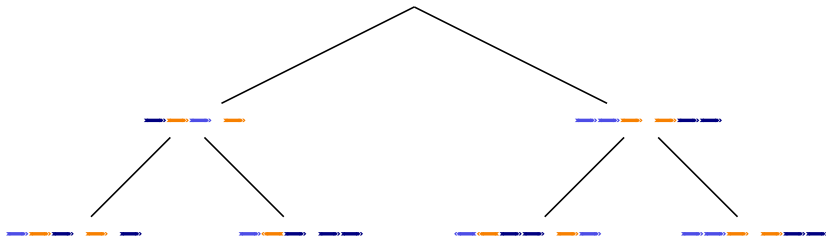
Small Parsimony for Natural Genomes



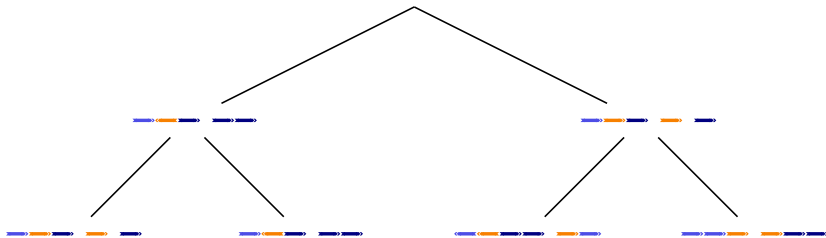
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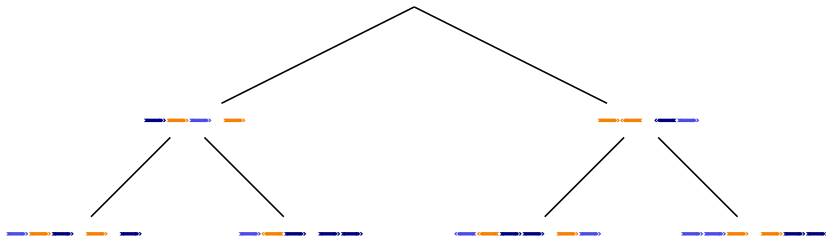
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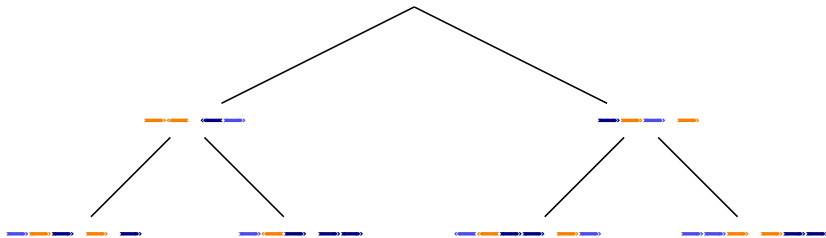
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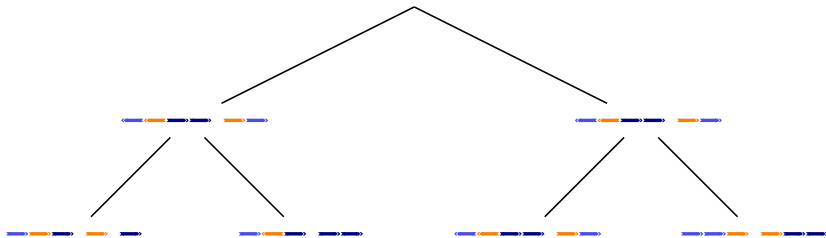
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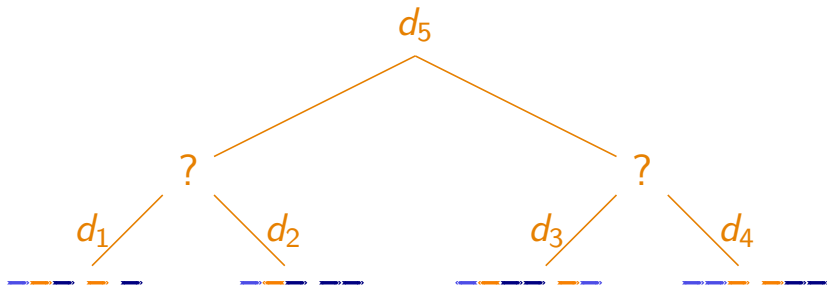


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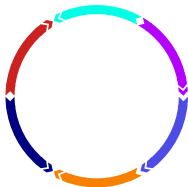


Small Parsimony for Natural Genomes

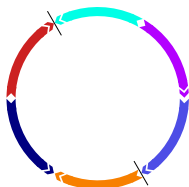
Minimize $d_1 + d_2 + d_3 + d_4 + d_5$



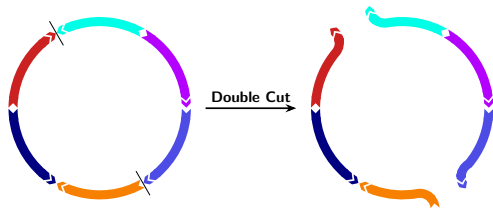
Model: Double-Cut-And-Join



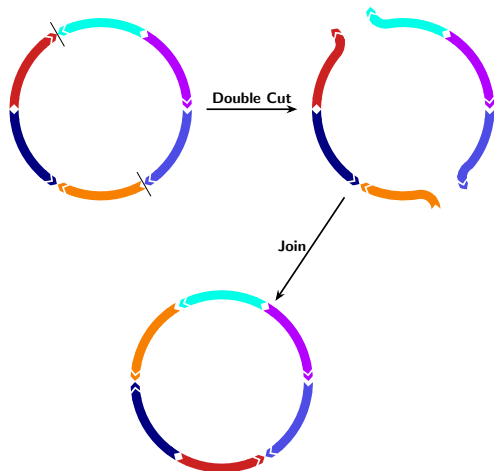
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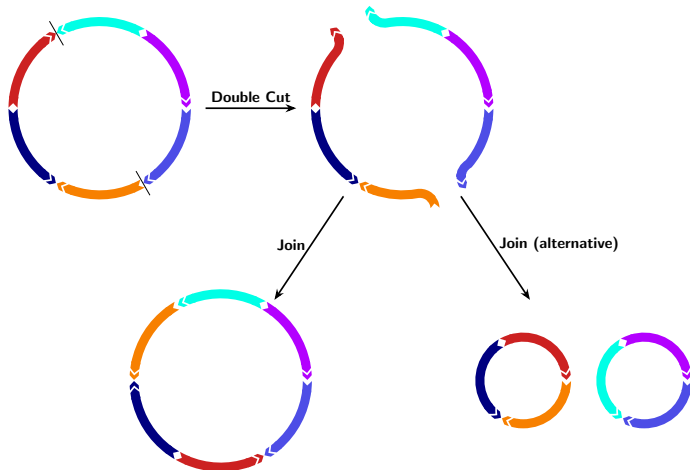
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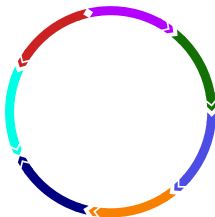
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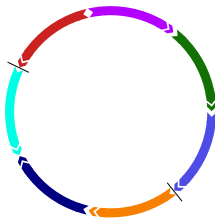
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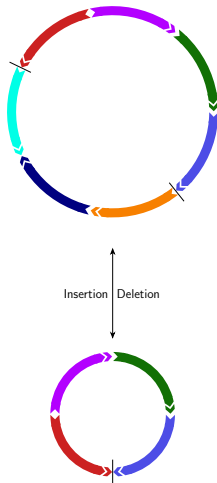
Insertions and Deletions



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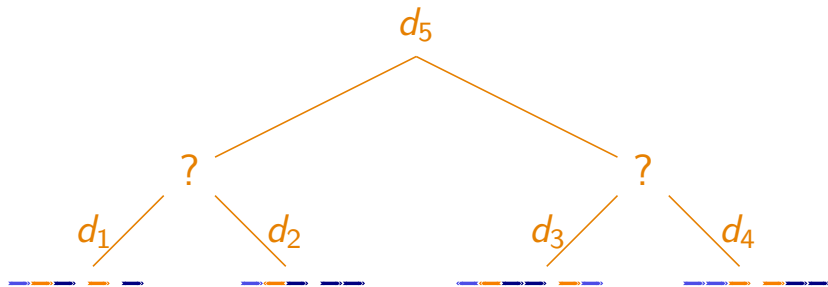


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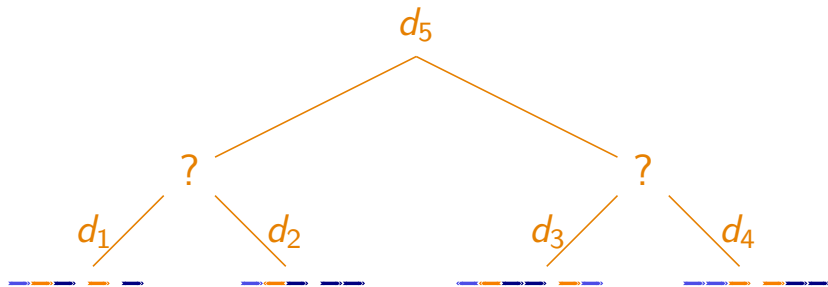
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Minimize $d_1 + d_2 + d_3 + d_4 + d_5$



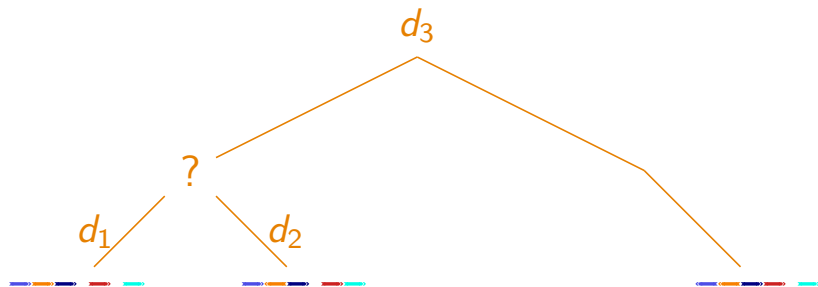
Small Parsimony for Natural Genomes

Minimize $d_1 + d_2 + d_3 + d_4 + d_5$

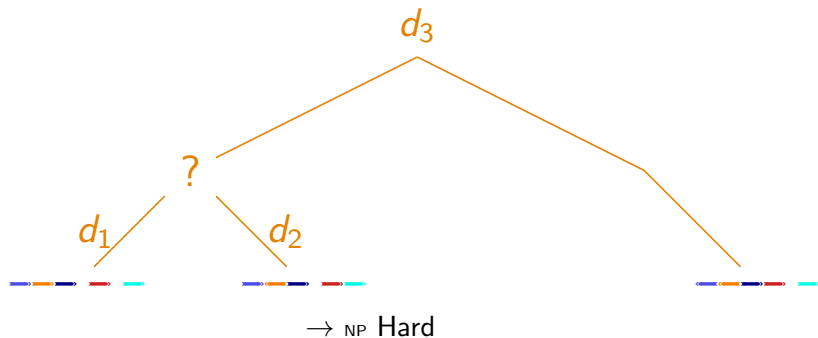


d_1, d_2, d_3, d_4, d_5 : (Minimum number of) DCJ and indel operations between the genomes.

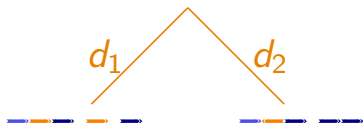
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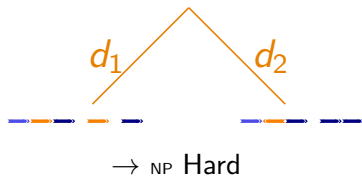
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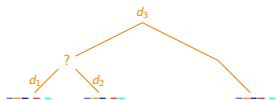
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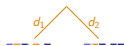
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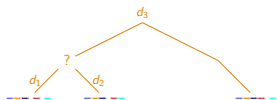


→ NP Hard

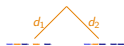


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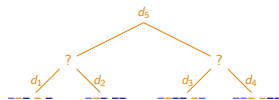
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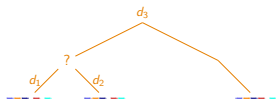
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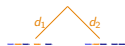
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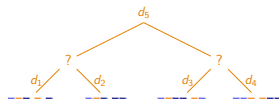
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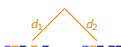


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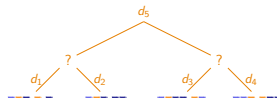
Small Parsimony for Natural Genomes



→ NP Hard



→ NP Hard



→ NP Hard

→ Solution via ILP

Integer Linear Programming (ILP)

Algorithm 1 Capping-free Small Parsimony

Objective

Minimize

$$\sum_{E \in E(T)} (\alpha \mathbf{f}_E + (\alpha - 1) \mathbf{w}_E)$$

Global level

For each genome $\mathbb{A} = (\mathcal{E} \cup \mathcal{T}, \mathcal{M} \cup \mathcal{A})$ of phylogeny T :

$$(C.01) \quad \mathbf{g}_u = \mathbf{g}_v \quad \text{with } (u, v) \in \mathcal{M}$$

$$(C.02) \quad \sum_{m \in F} \mathbf{g}_{m^h} \geq L_F^{\mathbb{A}} \quad \text{for each family } F$$

$$\sum_{m \in F} \mathbf{g}_{m^h} \leq H_F^{\mathbb{A}}$$

$$(C.03) \quad \sum_{uv \in \mathcal{A}} \mathbf{a}_{uv} = \mathbf{g}_v \quad \forall v \in \mathcal{E} \cup \mathcal{T}$$

Local level

For each edge $E = (\mathbb{A}, \mathbb{B}) \in E(T)$ with $\mathcal{CFMRD}(\mathbb{A}, \mathbb{B}) = (\mathcal{E} \cup \mathcal{T}, E_{\text{adj}}$

$E_{\text{ext}} \cup E_{\text{self}}$):

$$(C.04) \quad \mathbf{w}_E = \sum_{e \in E_{\text{adj}}} \mathbf{w}(e) x_e$$

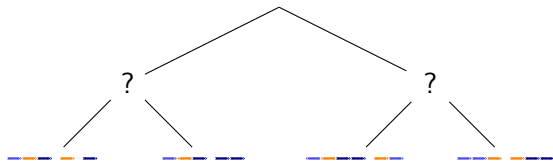
$$(C.05) \quad \mathbf{f}_E = \mathbf{n}_E - \mathbf{c}_E + \mathbf{q}_E + \mathbf{s}_E$$

$$(C.06) \quad \mathbf{n}_E = \frac{1}{2} \sum_{e \in E_{\text{ext}}} \mathbf{x}_e$$

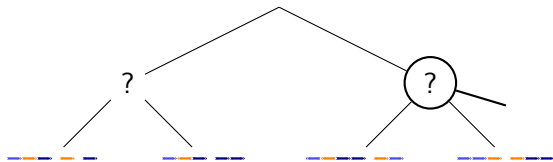
$$(C.07) \quad \mathbf{c}_E = \sum_{v \in \mathcal{E}} \mathbf{r}_v^c$$

$$(C.08) \quad 2\mathbf{q}_E \geq \mathbf{p}_E^{ab} + \mathbf{p}_E^{\max a} + \mathbf{p}_E^{\max b} - \mathbf{p}_E^{AB}$$

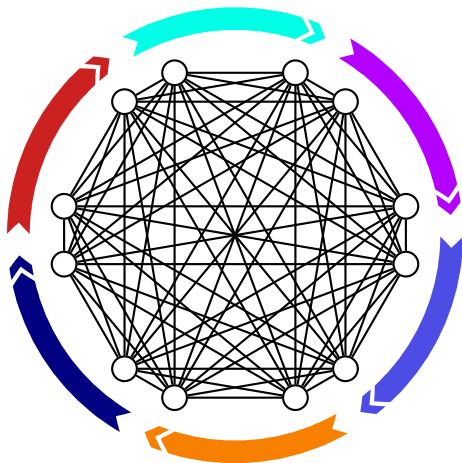
Vast Solution Space for Ancestral Adjacencies



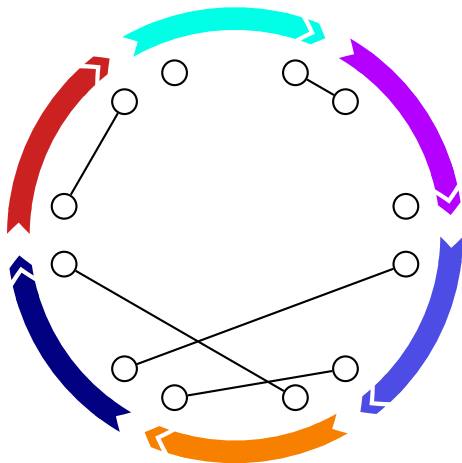
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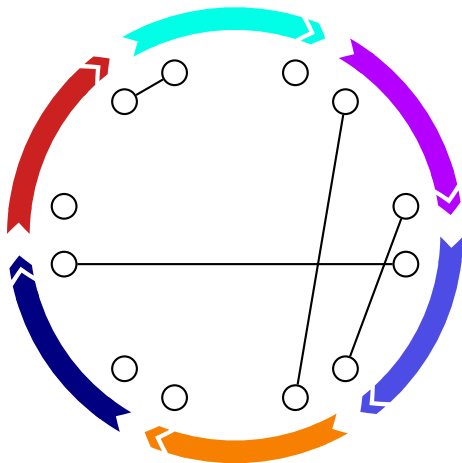
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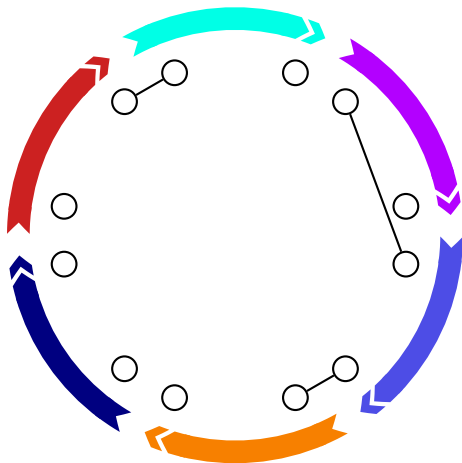
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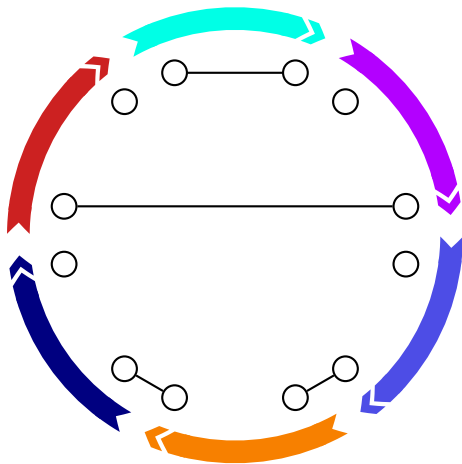
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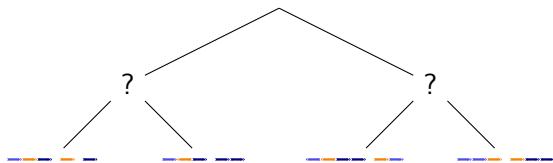
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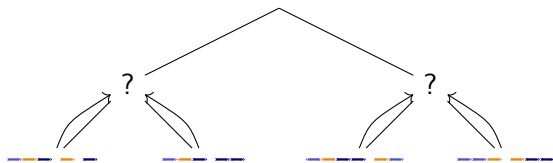
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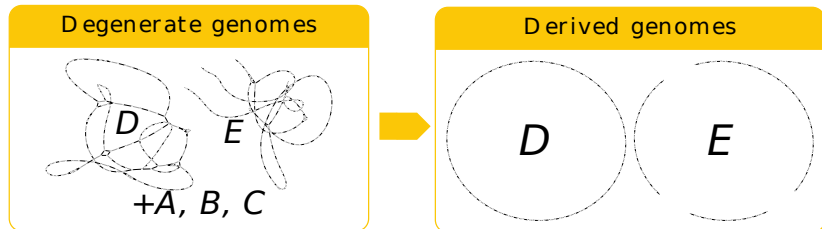
Heuristic Solution: Filter Adjacencies Based on Leafs



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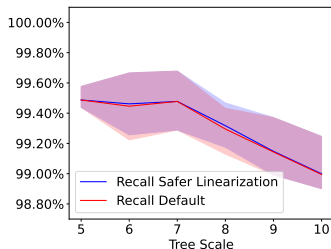
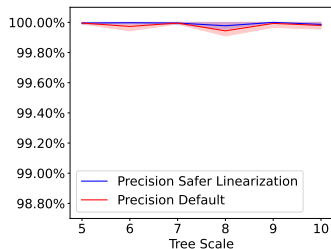
Degenerate Genomes



(Slightly) Adapted from (Doerr, Chauve, 2021).

Degenerate Genomes - the Good

On simulated data (ZOMBI+pre-filtering with DeCoSTAR), *if the ground truth adjacencies are represented in the degenerate genome*:



Degenerate Genomes - the Bad

- ▶ Good pre-filtering (DeCoSTAR) requires gene trees.



- ▶ Is not exact.

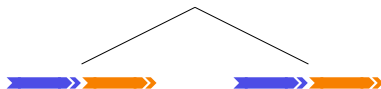


Our idea: Filter and Solver Tricks

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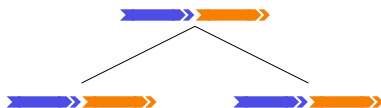
- ▶ Filter out adjacencies that are provably not needed.
→ Exploit features of the data:

Our idea: Filter and Solver Tricks



- ▶ Filter out adjacencies that are provably not needed.
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 - ▶ Conserved adjacencies at the leaves

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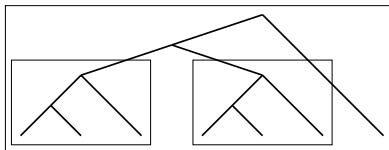
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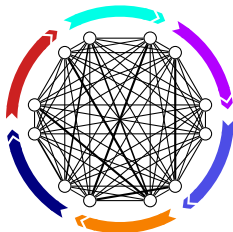
- ▶ Filter out adjacencies that are provably not needed.
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- ▶ Solver Tricks:
 - ▶ Good solutions are easily guessed → “warm start”
 - ▶ Solve progressively more complex versions of the problem:
 - ▶ Subtrees

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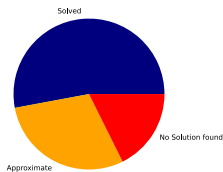
Extremely Preliminary Results

gurobi 12 on 1 thread with 1 hour time limit on all lineages (17)
with 20 leaves or fewer

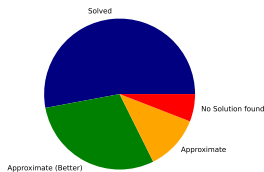
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Unoptimized



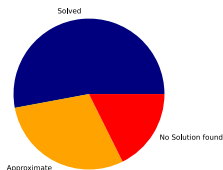
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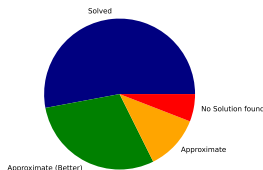
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- Main problem seems to be proving optimality.

SPP - Long Term Perspectives

- ▶ Transfer bounds from less complex (sub-) problems

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- ▶ Transfer bounds from less complex (sub-) problems
- ▶ ILP solving $\overset{?}{\Leftrightarrow}$ SAT solving
- ▶ SPP-variant that can model other types of events (horizontal transfers, chromosome duplication,...)
- ▶ Large Parsimony problem (no given tree)

CARP - A Specialized Problem for Pangenomes

Joint work with Jens Stoye

Quantifying Rearrangement Complexity in Pangenomes - Intuition

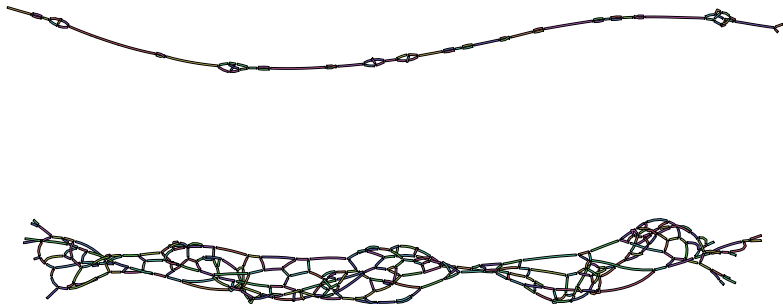


Image by courtesy of Luca Parmigiani

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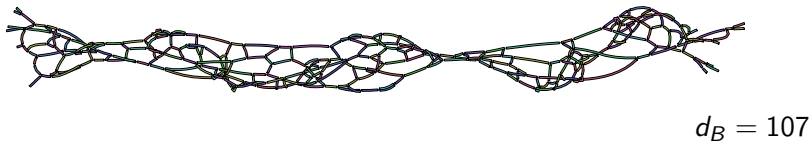
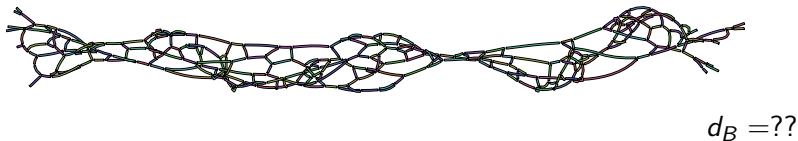


Image by courtesy of Luca Parmigiani

Quantifying Rearrangement Complexity in Pangenomes - Intuition



$$d_A < d_B$$



Quantifying Rearrangement Complexity in Pangenomes - Strategy



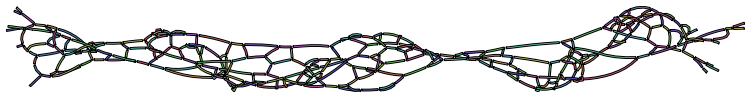
Quantifying Rearrangement Complexity in Pangenomes - Strategy

~~Boring~~ **Simple Pangenome**



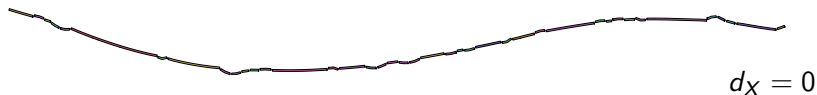
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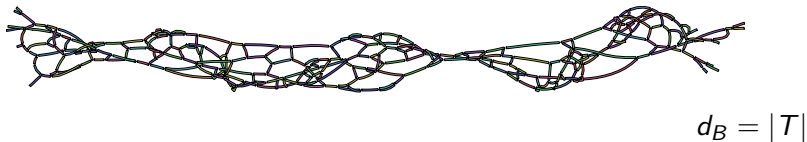


Quantifying Rearrangement Complexity in Pangenomes - Strategy

~~Boring~~ **Simple Pangenome**



Transform by operations T



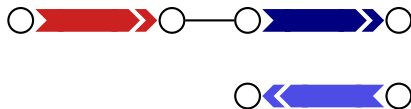
Multi-Breakpoint Graph (MBPG)



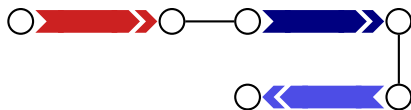
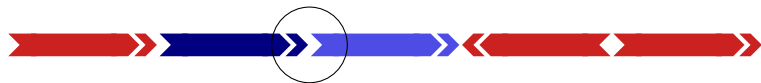
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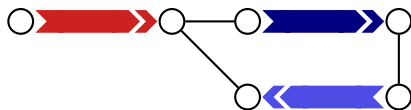
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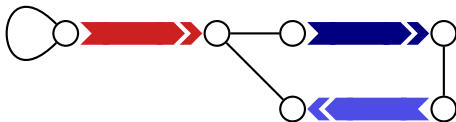
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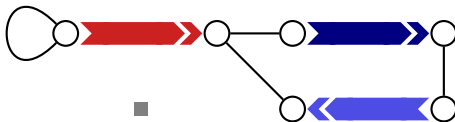
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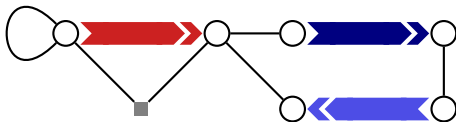
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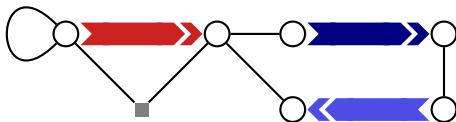
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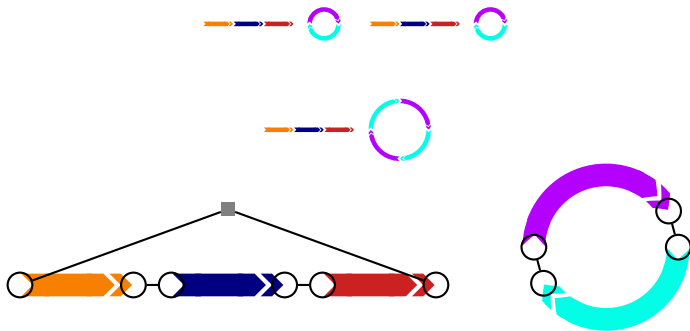


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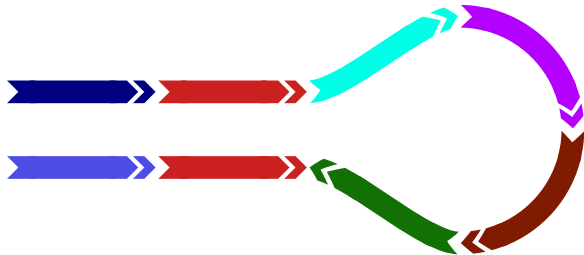
- ▶ GFA format (w/o sequence) can be represented as an MBPG
- ▶ Note: We still assume local variants have been filtered

MBPG of a Simple Pangenome

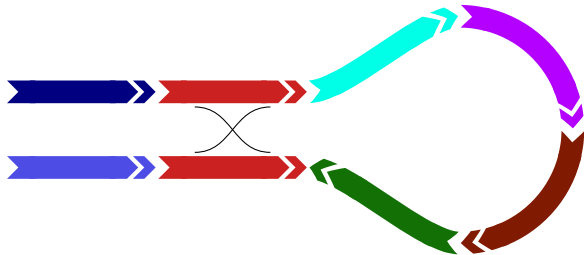


- Simple pangenome \iff adjacencies are a perfect matching

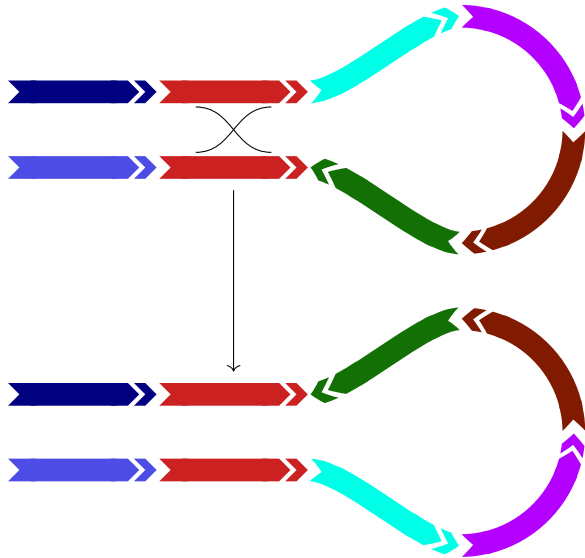
Rearrangements and Homologous Recombinations



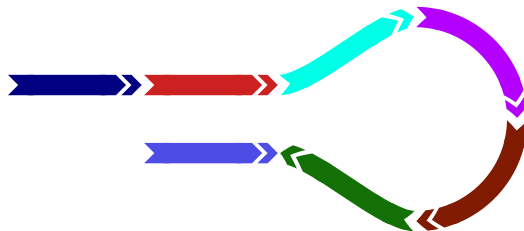
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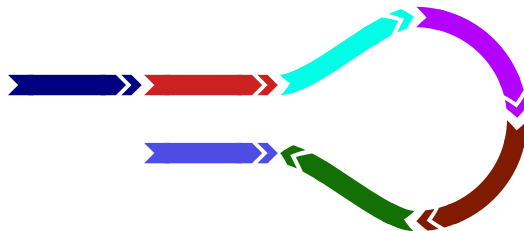
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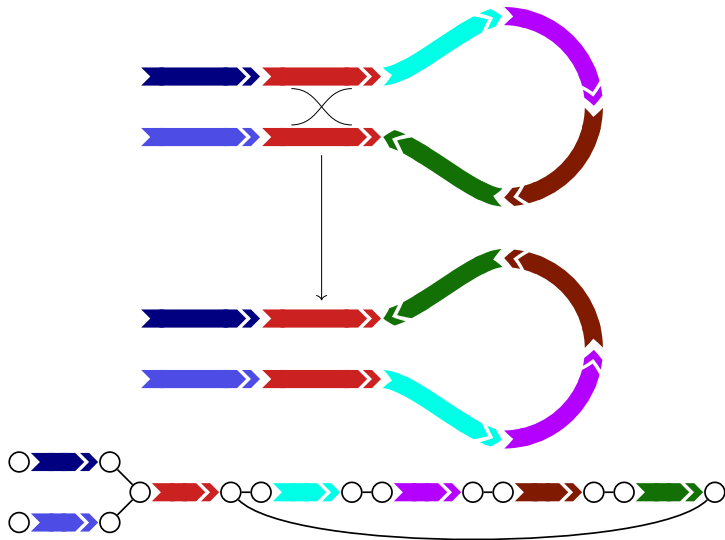


Rearrangements and Homologous Recombinations



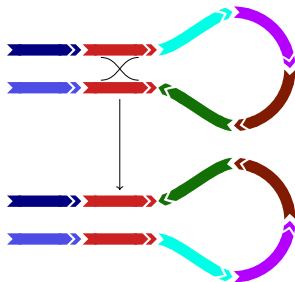
- ▶ No rearrangements via Homologous Recombination.

MBPG and Homologous Recombinations

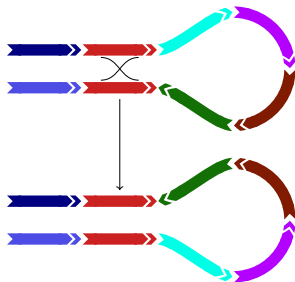


- Homologous Recombinations don't change the graph!

(Non)-Adjacency Modifying Operations

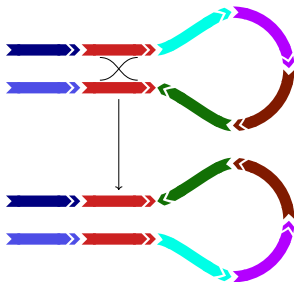


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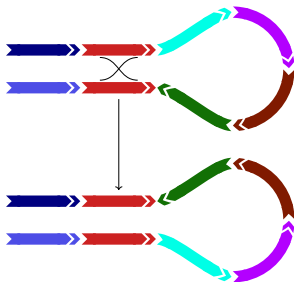
- No change in adjacencies!

(Non)-Adjacency Modifying Operations



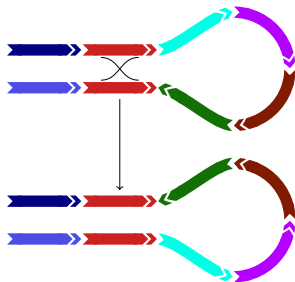
- No change in adjacencies!
→ Non-Adjacency Modifying Operations (Namos)

(Non)-Adjacency Modifying Operations



- No change in adjacencies!
 - Non-Adjacency Modifying Operations (Namos)
 - ↔ Adjacency Modifying Operations (Amos)

(Non)-Adjacency Modifying Operations



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Amos can introduce structural complexity!

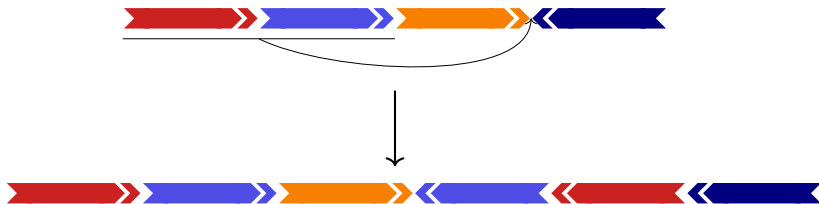
Amos - Example: Segmental Duplication



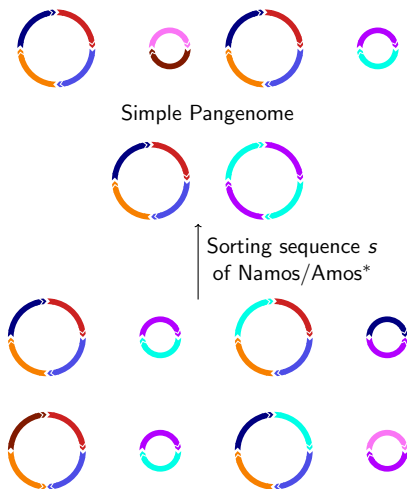
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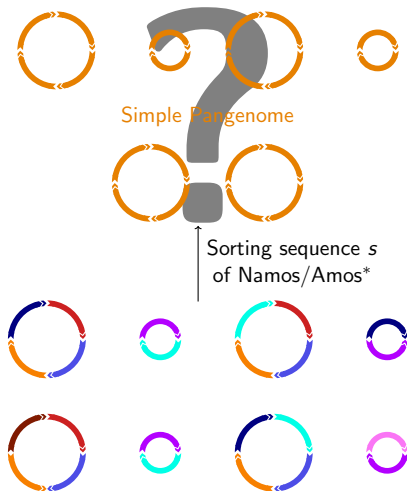
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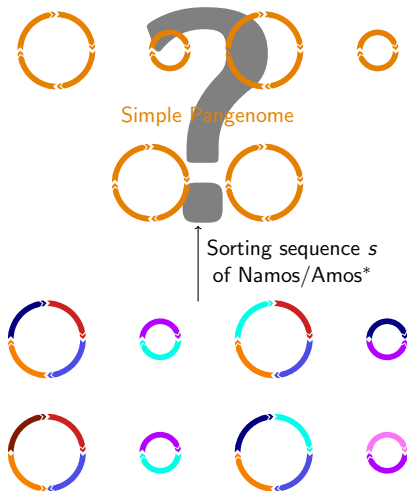
General Ancestral Reconstruction Problem (GARP)



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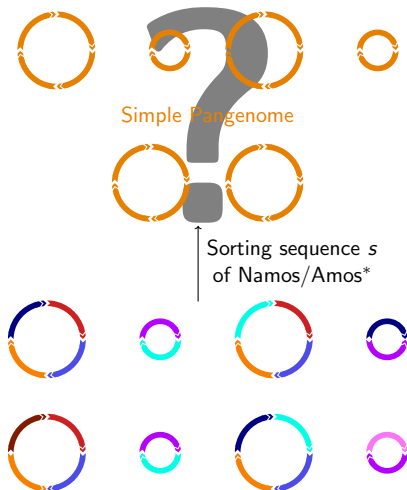


General Ancestral Reconstruction Problem (GARP)



- #Amos in s : measure of the Structural Complexity.

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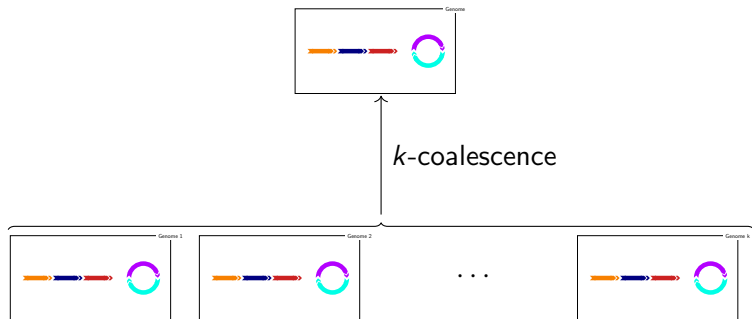


- ▶ $\#Amos$ in s : measure of the Structural Complexity.
- ▶ * with minimal $\#Amos$

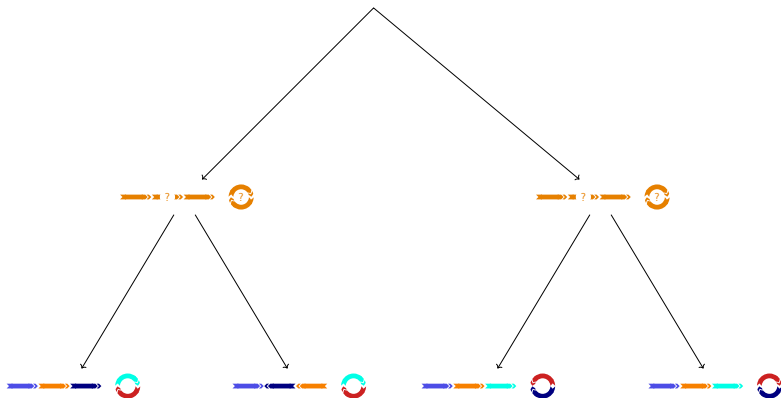
k -Coalescence – an important Namo



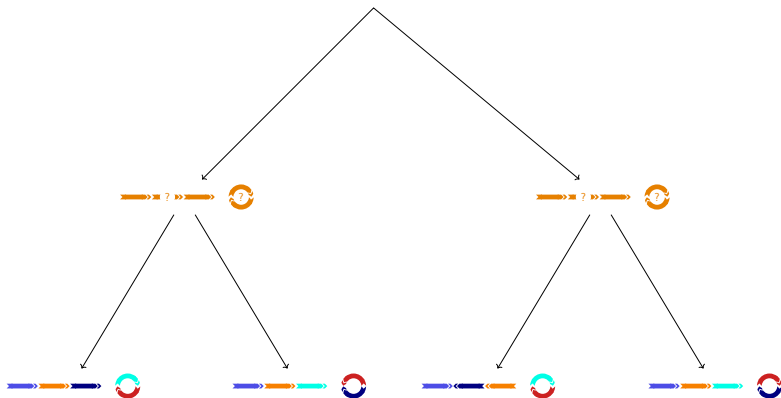
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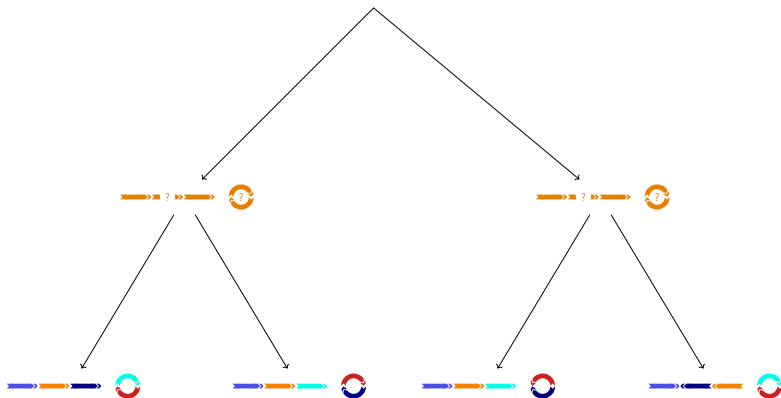
Large Parsimony Problem and GARP



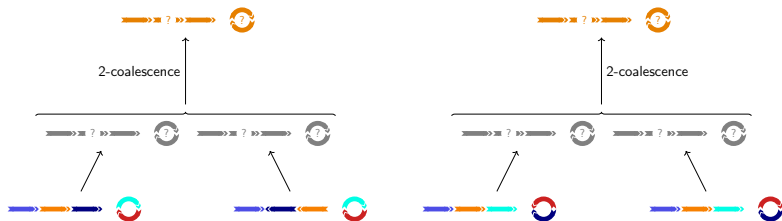
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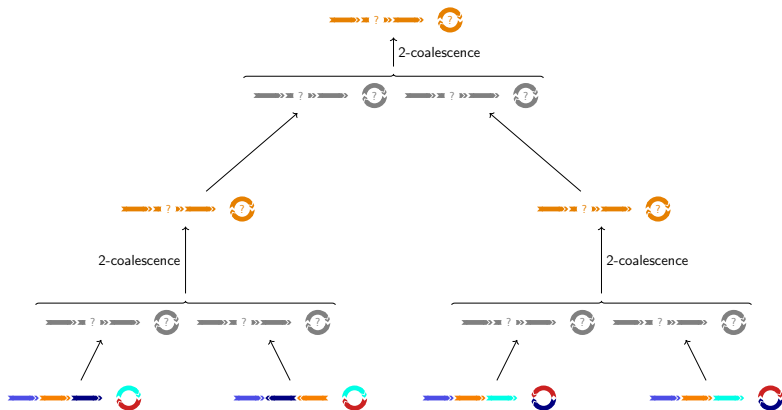
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Large Parsimony Problem and GARP



GARP and Classical Problem Formulations

Problem name	Given genomes	Classical Formulation	Namos (N)
Distance problem	Genomes X, Y on the same marker set (single copy)	Find the minimum number of operations in M to transform X to Y .	– (2-coalescence)
Median problem	Genomes X_1, \dots, X_k on the same marker set (single copy)	Find a genome Y that minimizes the total distance to X_1, \dots, X_k .	– (k -coalescence)
Large parsimony	Genomes X_1, \dots, X_k on the same marker set (single copy)	Find a binary tree with leaves X_1, \dots, X_k that minimizes the total distance between the genomes at each edge.	2-coalescence

► Very limited interaction between genomes (mostly coalescence, sometimes chromosome (de-)duplication)

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- ▶ Pangenomes → phylogenetic closeness → more interaction/horizontal effects
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- For a lower bound, we need a “maximally powerful” set of Namos

Observations from the MBPG

Observation

Given a Name o and pangenomes \mathbb{P}, \mathbb{P}' , where $\mathbb{P} \xrightarrow{o} \mathbb{P}'$, the MBPGs of \mathbb{P} and \mathbb{P}' are identical.

Observations from the MBPG

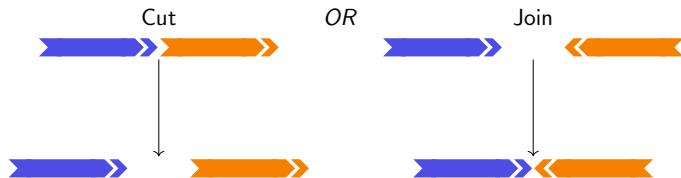
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Definition

A set of Namos N is called MBPG-complete, if for all pairs of pangenomes \mathbb{P}, \mathbb{P}' with the same MBPG there is a sequence of Namos $o_1 o_2 \dots o_k \in N^*$, such that $\mathbb{P} \xrightarrow{o_1} \xrightarrow{o_2} \dots \xrightarrow{o_k} \mathbb{P}'$.

SCJ - A simple Amo



SCJ-CARP Theoretical result

- ▶ SCJ Large Parsimony is NP-hard

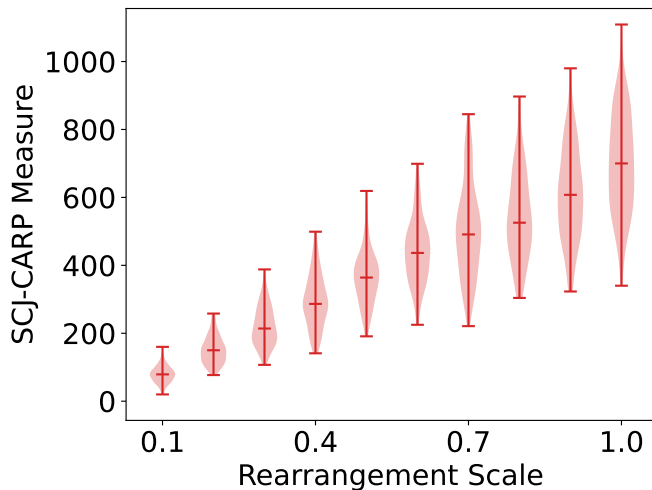
SCJ-CARP Theoretical result

- ▶ SCJ Large Parsimony is NP-hard
- ▶ However SCJ-CARP:

Lemma

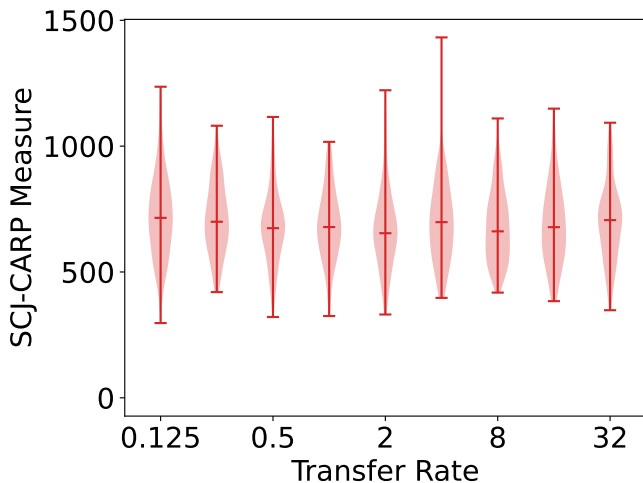
One needs exactly $|E_C|$ SCJs to transform a pangenome into a simple one where $E_C \subset E_A$ is a subset of adjacency edges that can be determined in linear time.

SCJ-CARP Tracks Rearrangements



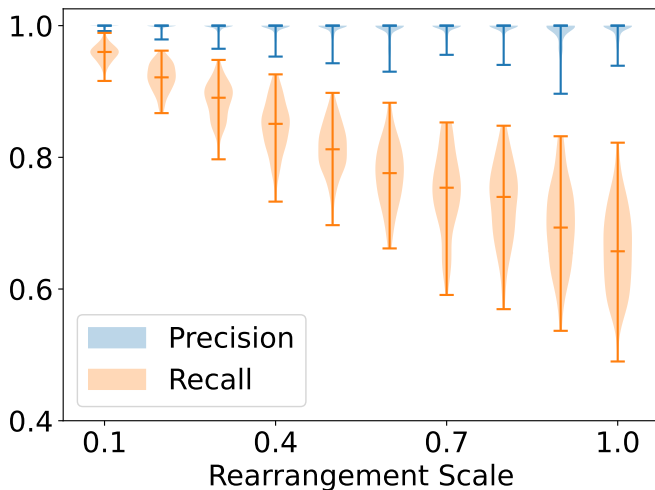
Pearson Coefficient: 0.88

SCJ-CARP Does Not Track Horizontal Effects



Pearson Coefficient: -0.01

SCJ-CARP Reconstructs Ancestral Adjacencies (to a Limited Extent)



CARP- Long Term Perspectives

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- ▶ Weighted Namos

Conclusion

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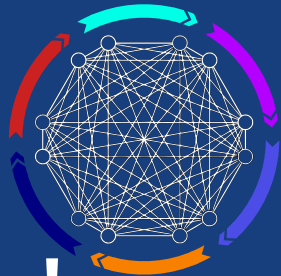
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- ▶ There is a wealth of theoretical results for rearrangements that only need slight adaptations to make them useful in practice.
- ▶ Future work: (Formal definition for) Marker segmentation on pangenomes

Thank you!



slides

