On the consistency of orthology relationships

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ALGCO seminar

Introduction

- Joint work with Christophe Paul(LIRMM) and Céline Scornavacca (Institut Des Sciences De L'volution De Montpellier).
- Orginally presented at RECOMB Comparative Genommics Workshop.
- Main result: A polynomial time algorithm for resolving orthology data between genes in a way that is consistent (i.e. can be made to fit with a species tree).

Evolution of Species vs Genes

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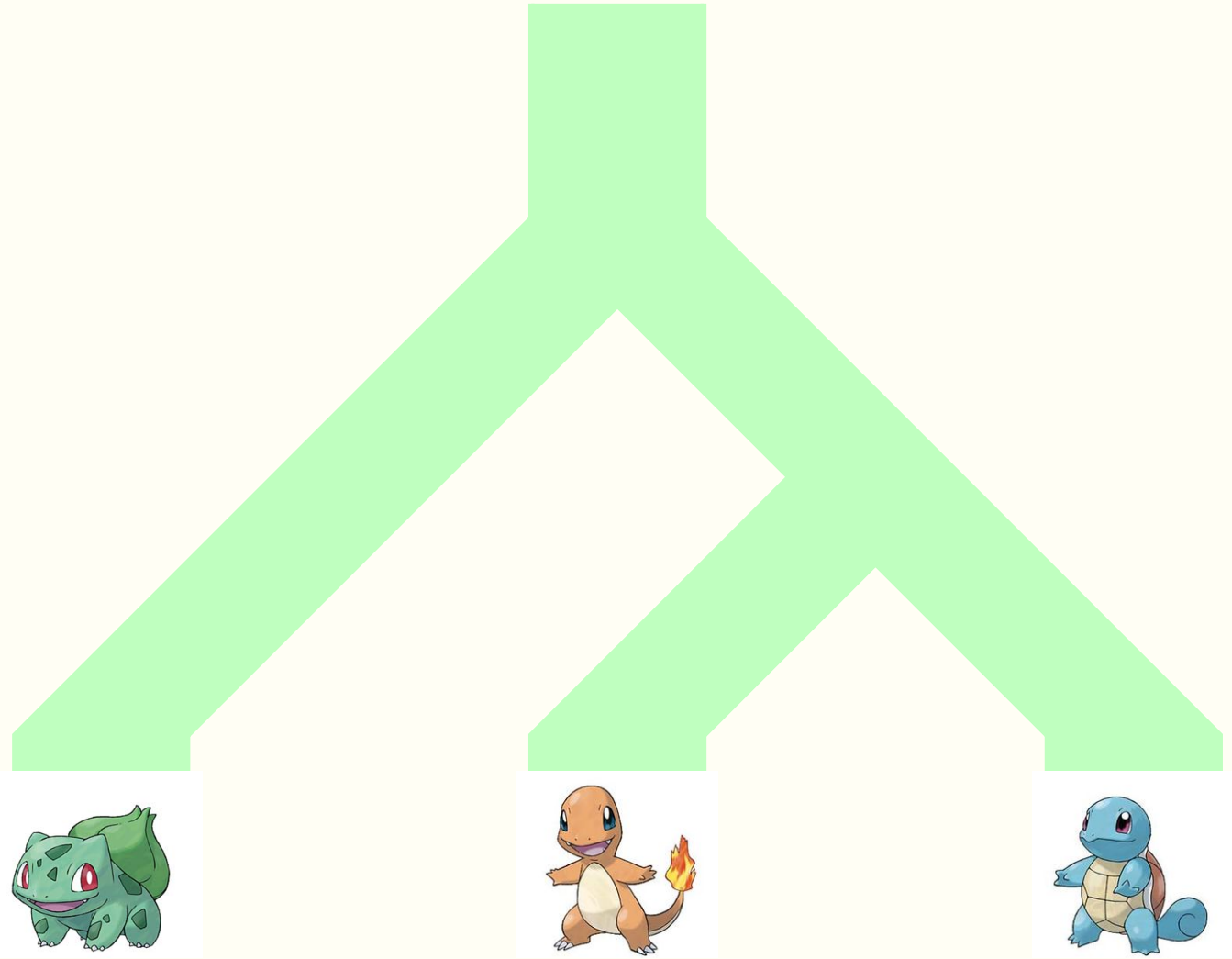

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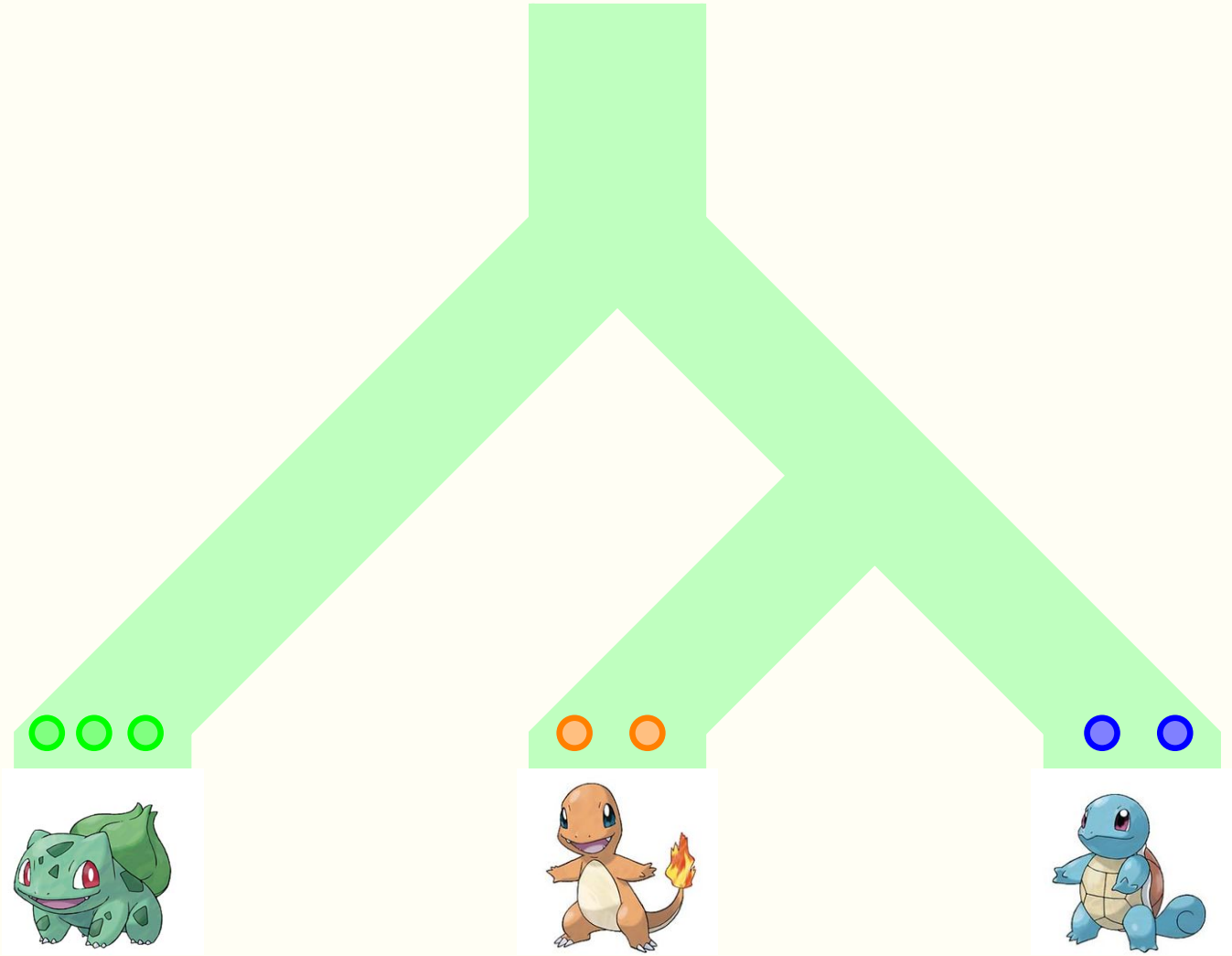

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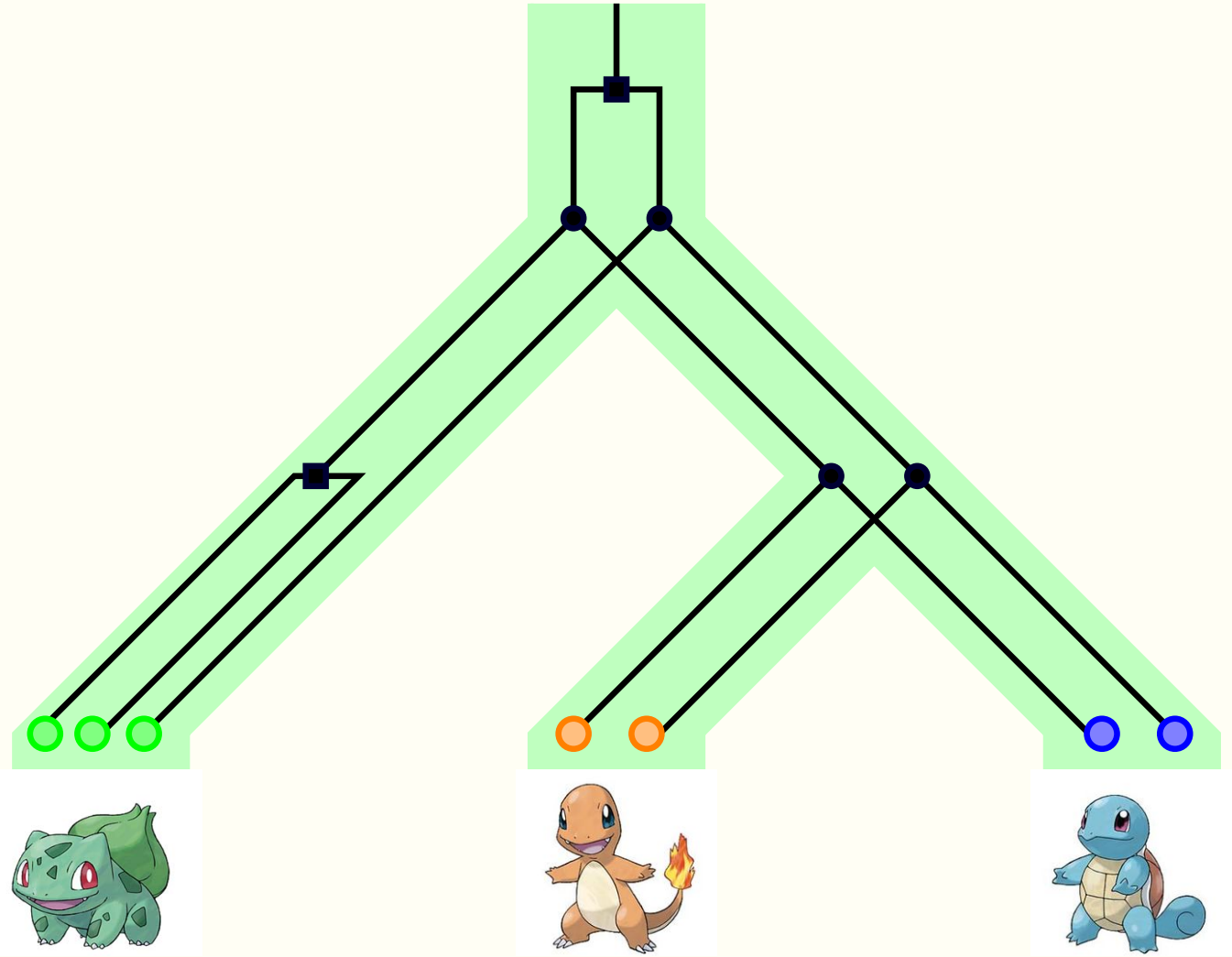

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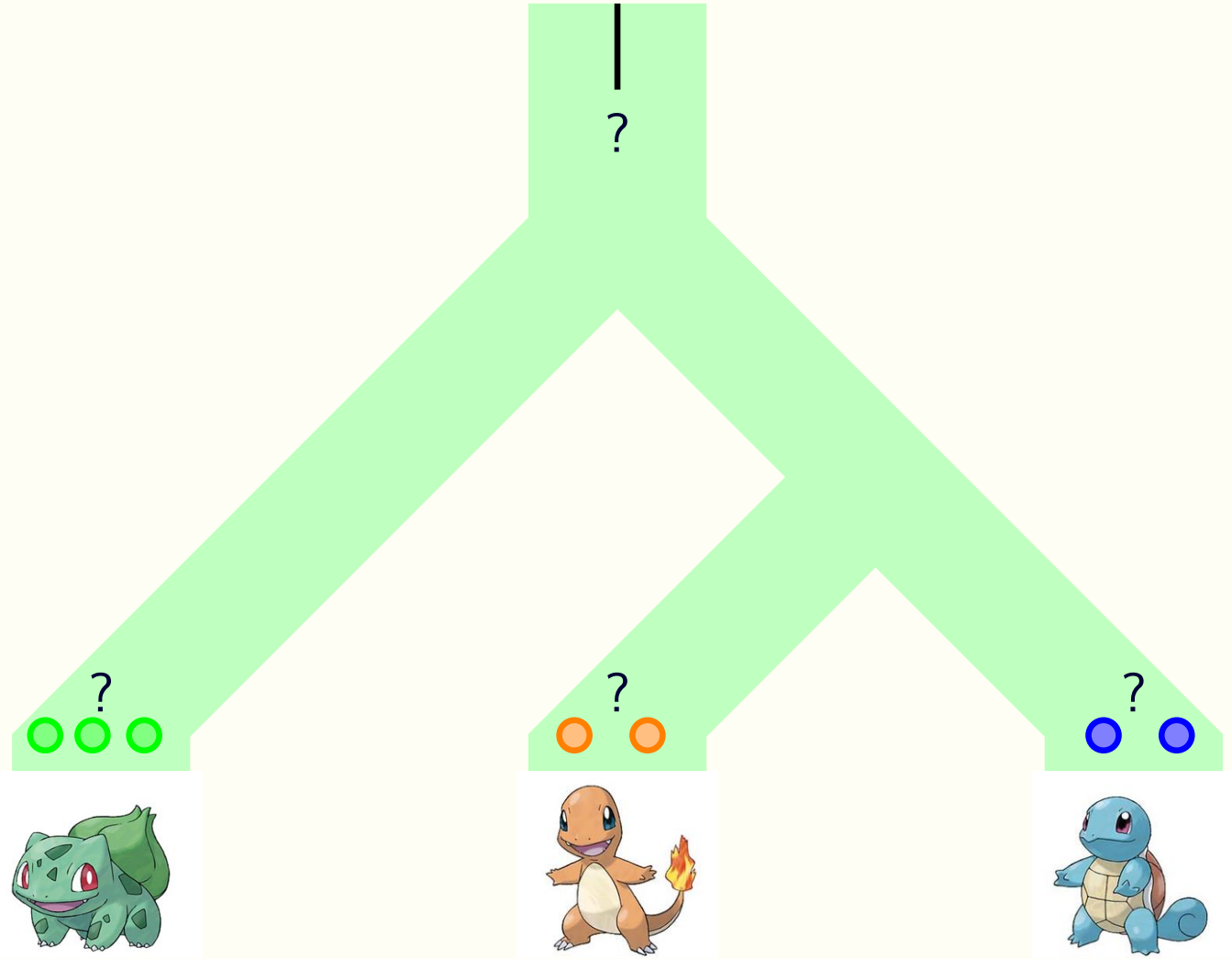

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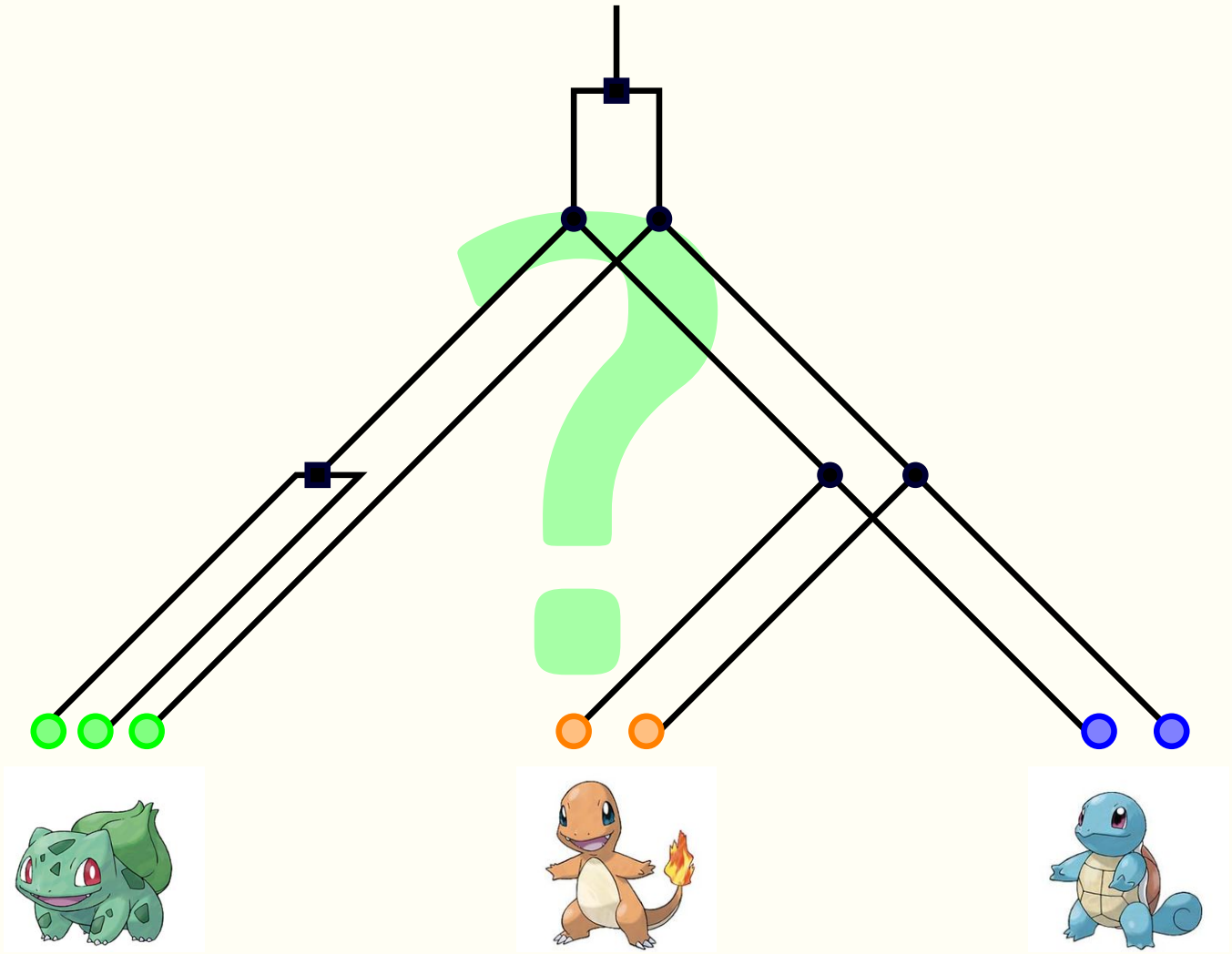

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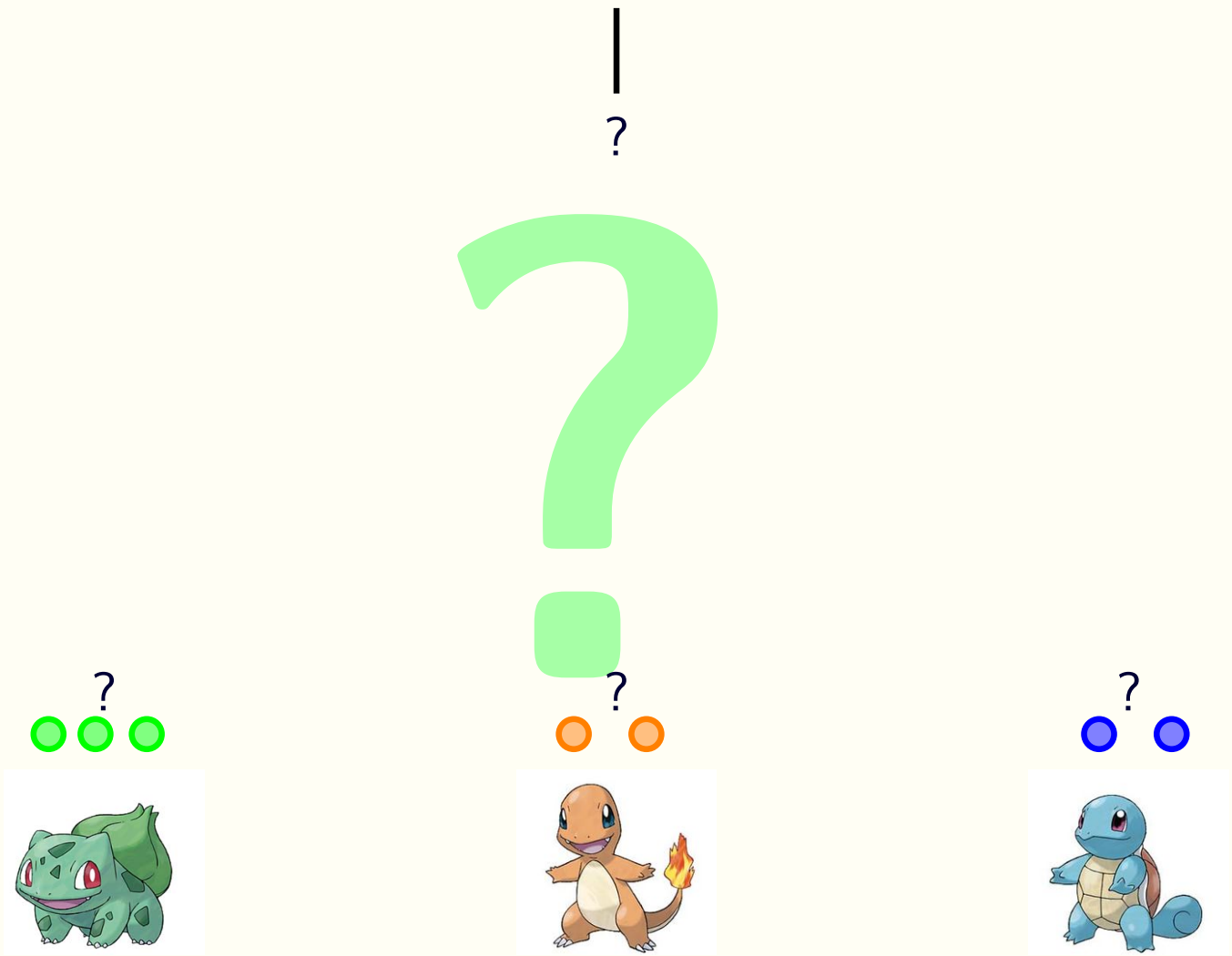
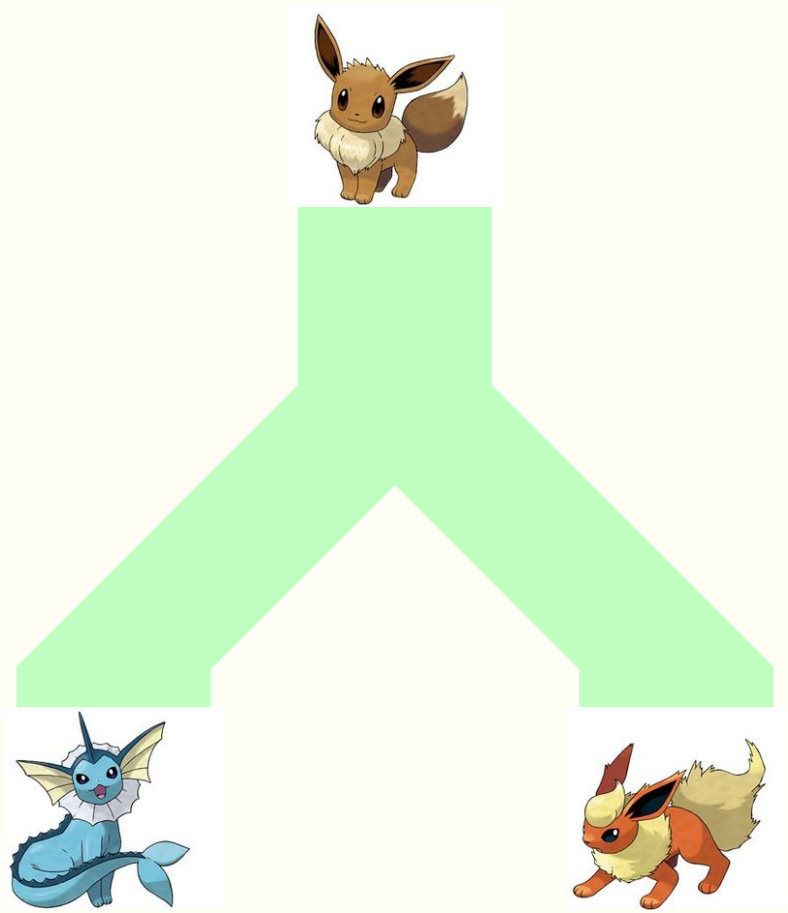


Propagation of genes: Speciation



- A **speciation** event occurs when an ancestor species passes a copy of each of its genes onto its descendants.
- A pair of genes are **orthologs** if they are most closely related by a speciation event.

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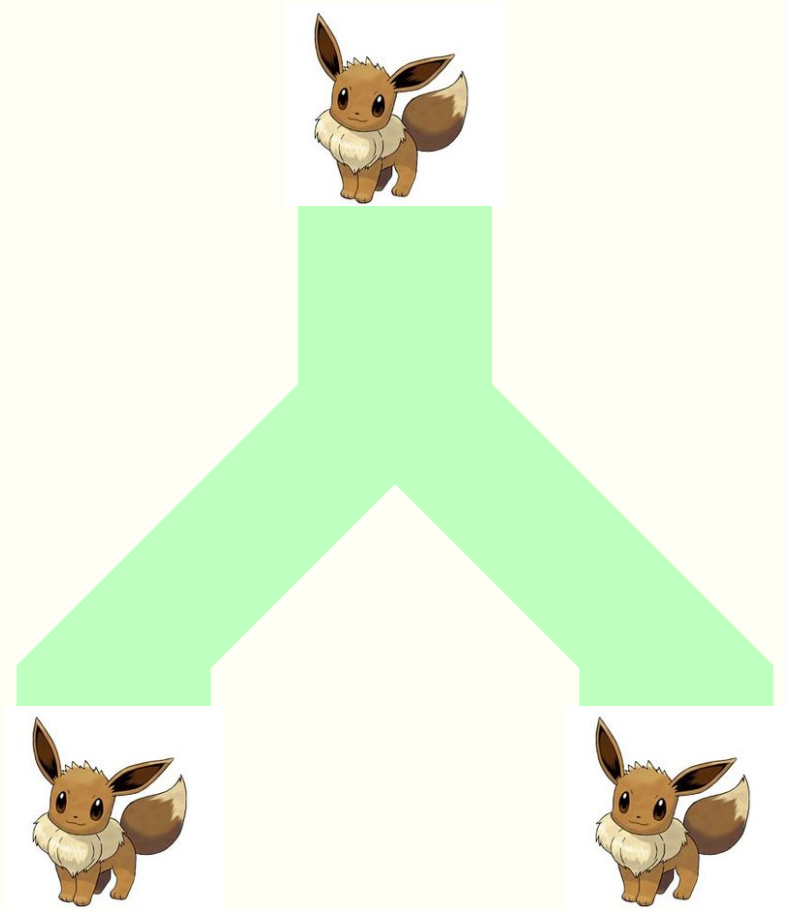

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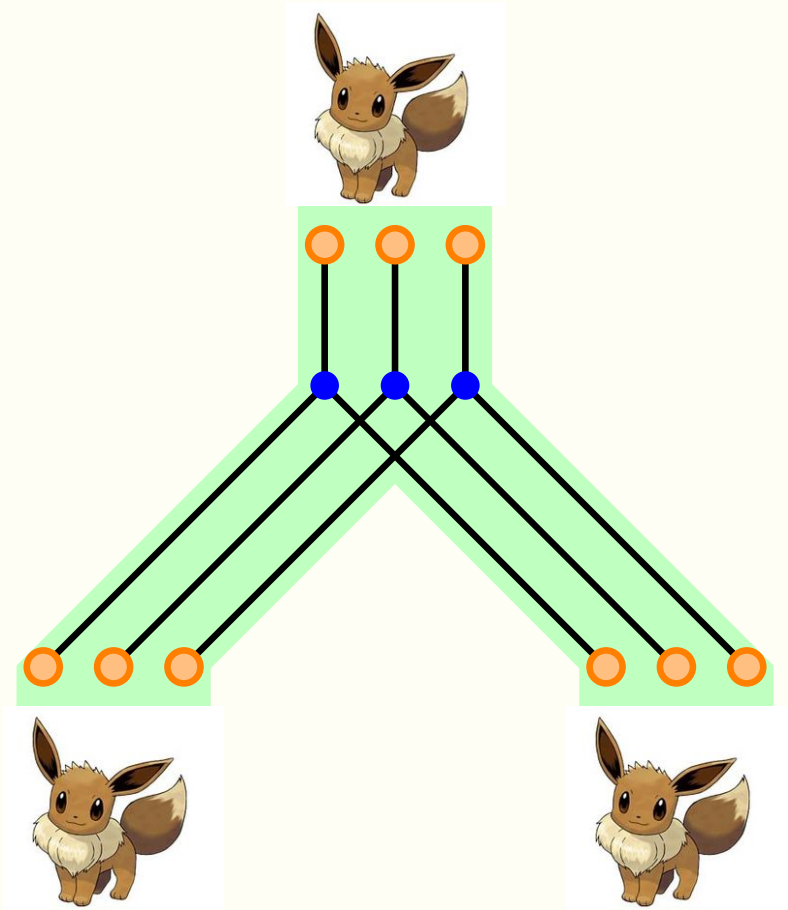

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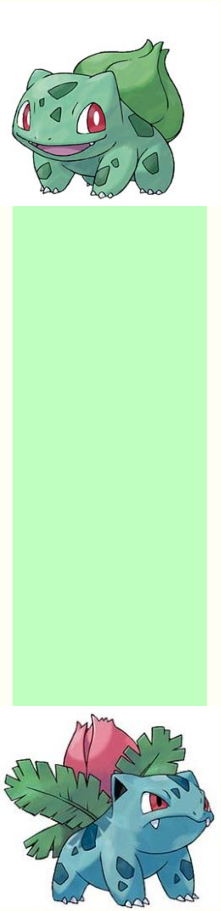

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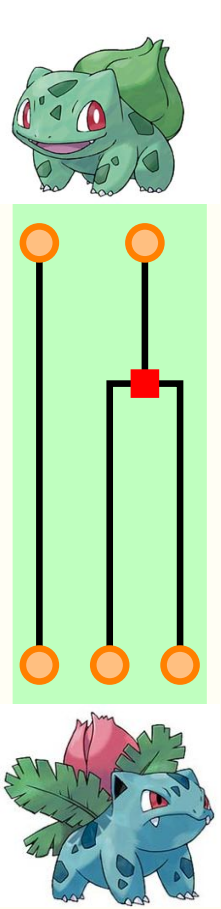

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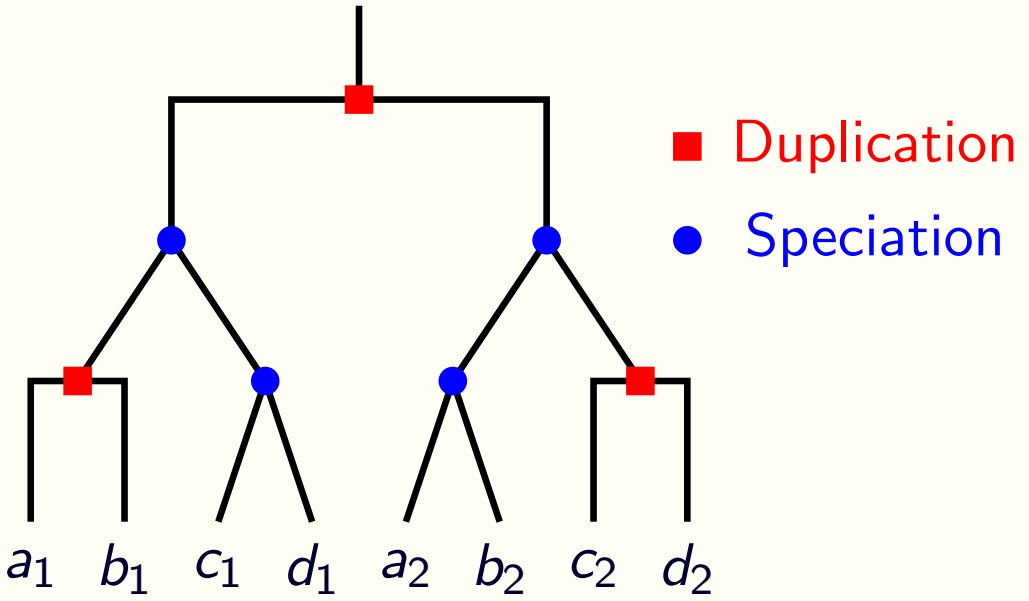
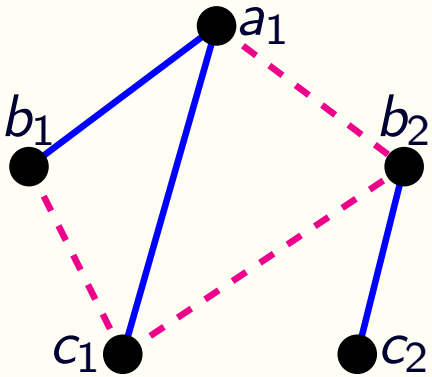
Orthologs vs paralogs



- We depict the evolutionary history of a set of genes with a **DS-tree**.
- Two genes are **orthologs** if they are related by a speciation event, and **paralogs** if they are related by a duplication event.
- Useful for functional analysis - orthologs tend to perform similar functions, paralogs tend to differ.

Constraint Graphs



- A **constraint graph** $G = (V, E \cup \mathit{Unknown})$ represents the known orthology / paralogy relations between pairs of genes.
- Solid edges = known orthologs; non-edges = known paralogs; dashed edges = unknown.

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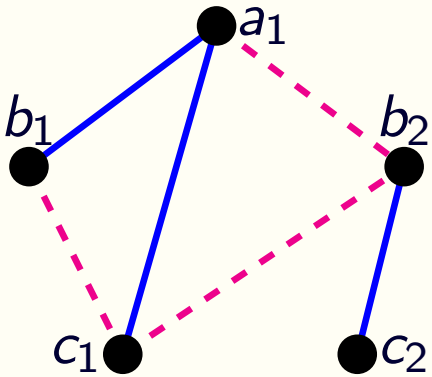

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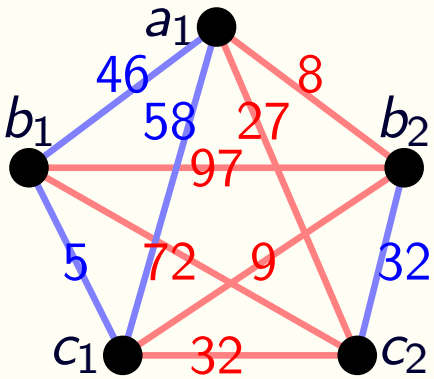

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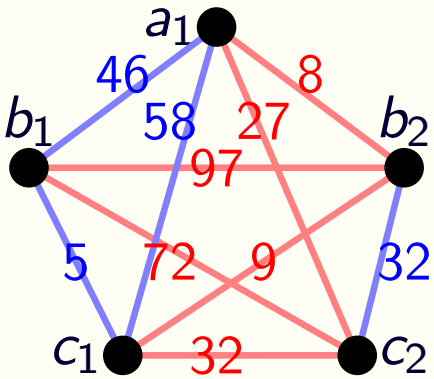

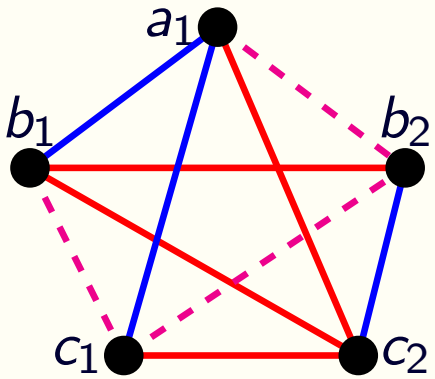

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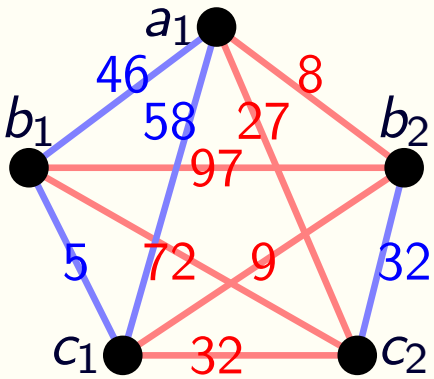

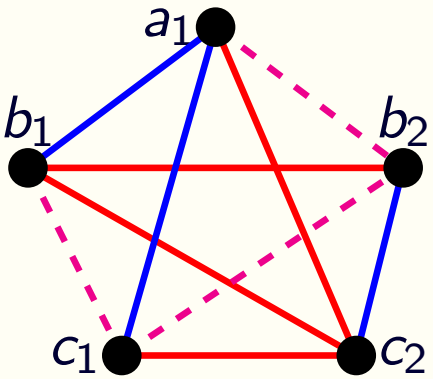

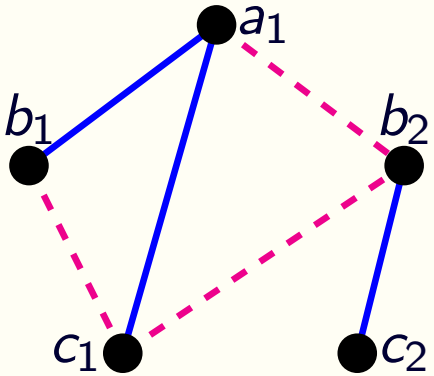

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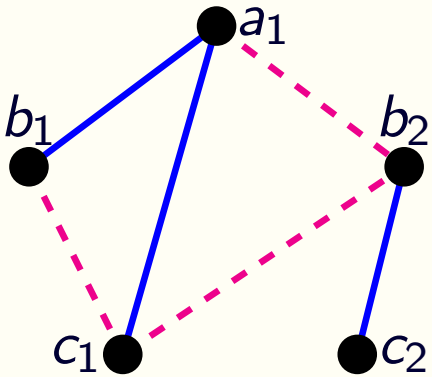
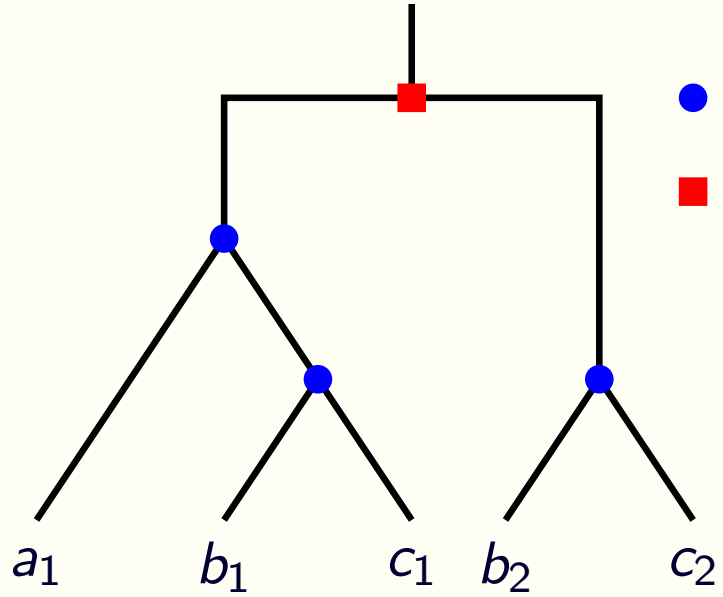
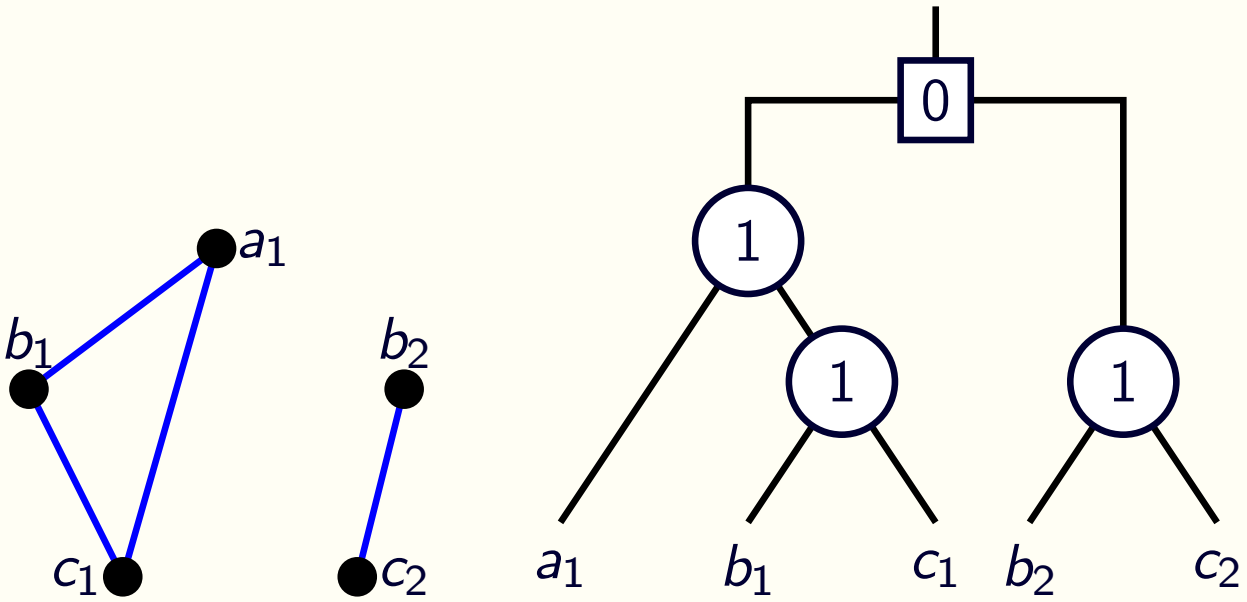




- Speciation
- Duplication

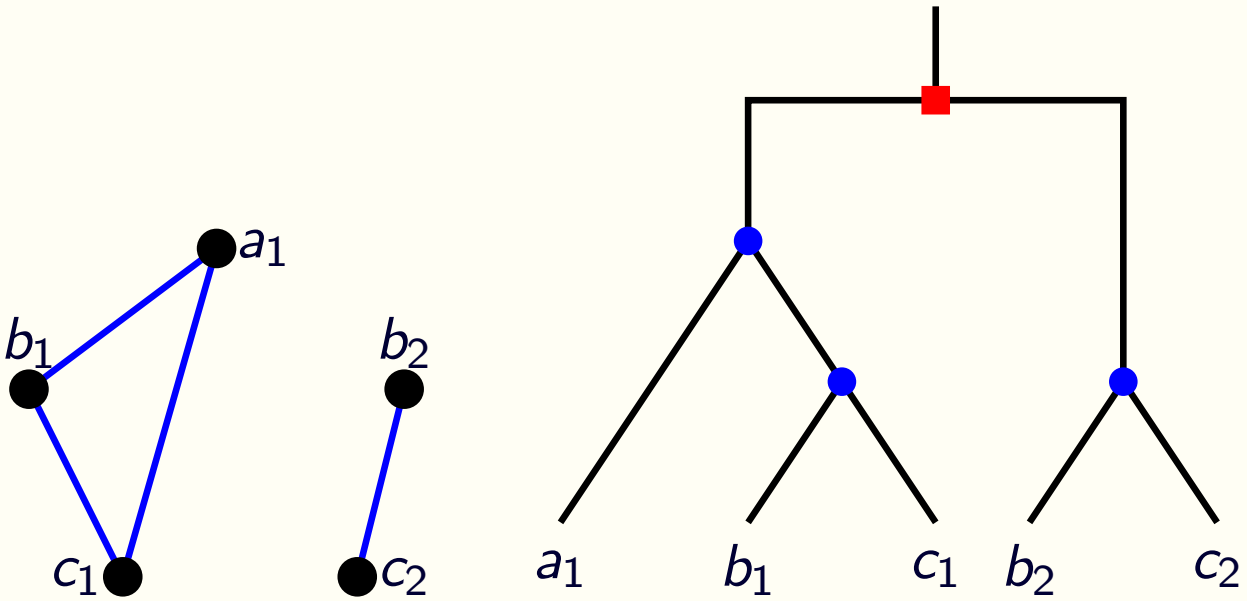
- Given a constraint graph, we wish to find an evolutionary history for the set of genes.
- A **DS-tree** (Duplication/Speciation tree) is a rooted tree over a set of genes, with internal nodes labelled as **duplication** events (red squares) or **speciation** events (blue circles).
- A DS-tree T **satisfies** a constraint graph C if for every pair of known orthologs are related by a speciation event, and every pair of known paralogs are related by a duplication event.

Relation to cographs



- A graph G with a vertex set V is a **cograph** if there exists a **co-tree** T with leaf set V, internal nodes labelled 0 or 1, such that two vertices are adjacent in G iff their l.c.a. in T with label 1.

Relation to cographs



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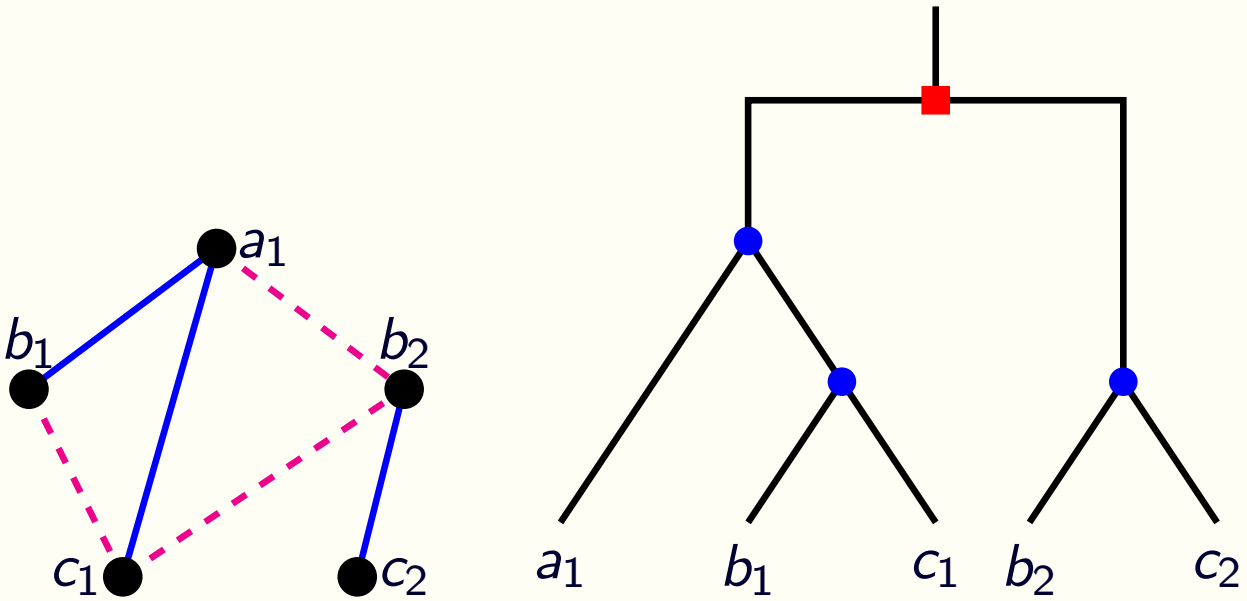

- Co-trees are equivalent to (binary) co-trees.
- Finding a DS-tree satisfying a constraint graph is equivalent to the Cograph Sandwich Problem (polynomial-time solveable[1]).

[1] Golumbic, M., Kaplan, H., Shamir, R.: Graph sandwich problems. Journal of Algorithms (1995)

Finding a DS-tree for a cograph

Cotree($G = (V, E)$):

1 **If** G is disconnected:
2 Find partition $V = V_1 \uplus V_2$ such that $V_1 \times V_2 \cap E = \emptyset$;
3 Set $root.type = Dup$;
4 $root.add\_child(\text{Cotree}(G[V_1]))$;
5 $root.add\_child(\text{Cotree}(G[V_2]))$;
6 **Return** $root$;
7 **Else**:
8 Find partition $V = V_1 \uplus V_2$ such that $V_1 \times V_2 \subseteq E$;
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Exception: If no partition found, G is not a cograph
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Checking if a constraint graph has a DS-tree

SandwichCograph($G = (V, E \cup \mathit{Unknown})$):

1 **If** $G[E]$ is disconnected:
2 Find partition $V = V_1 \uplus V_2$ such that $V_1 \times V_2 \cap E = \emptyset$;
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4 **Else**:
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6 Set $\mathit{root}.\mathit{type} = \mathit{Spec}$;
7 $\mathit{root}.\mathit{add\_child}$(SandwhichCograph($G[V_1]$));
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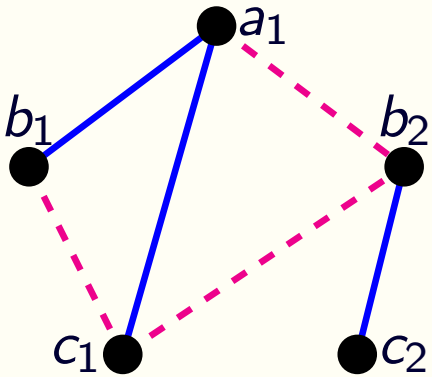
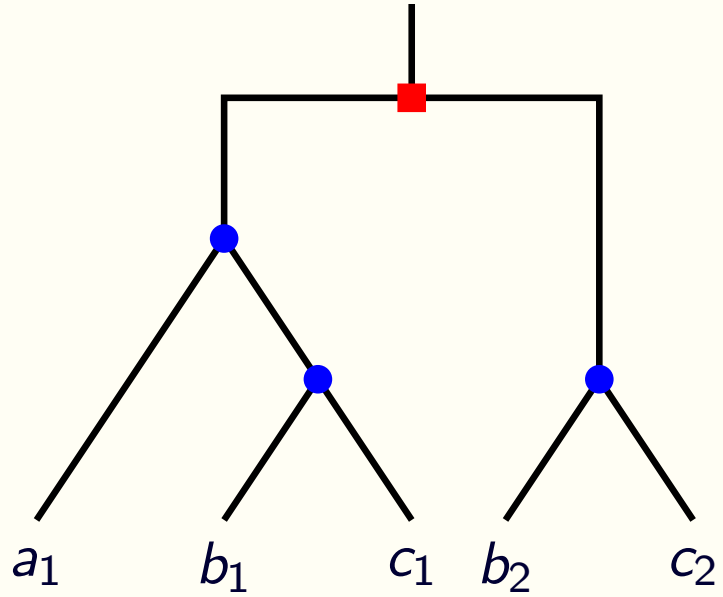
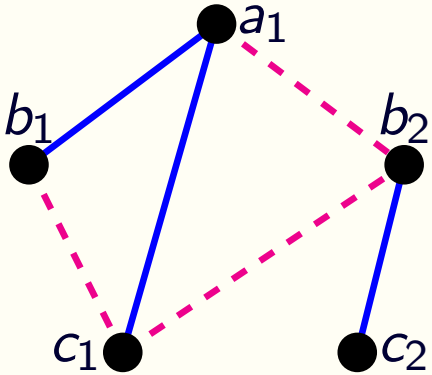
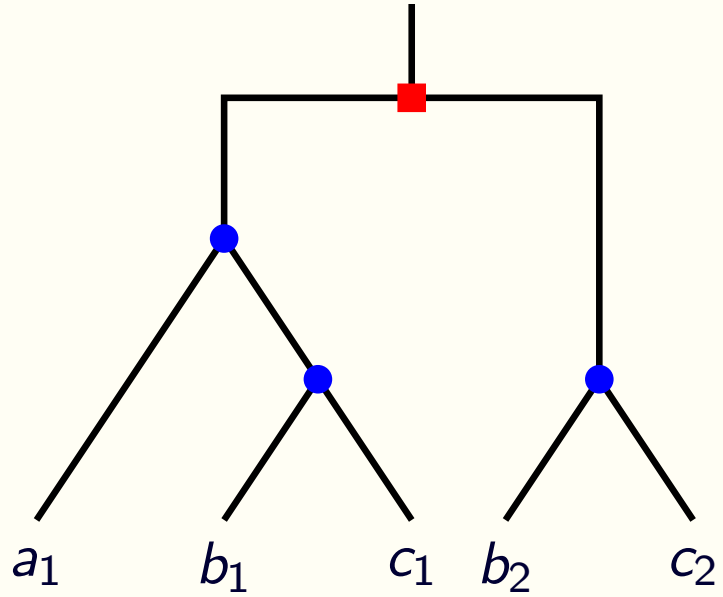




- A DS-tree T **satisfies** a constraint graph $G = (V, E \cup \mathit{Unknown})$ if for every pair of known orthologs are related by a speciation event, and every pair of known paralogs are related by a duplication event.
- Finding a DS-tree satisfying a constraint graph can be done in polynomial time.
- HOWEVER...
- ... not every DS-tree satisfying G is a good solution.

Finding a DS-tree





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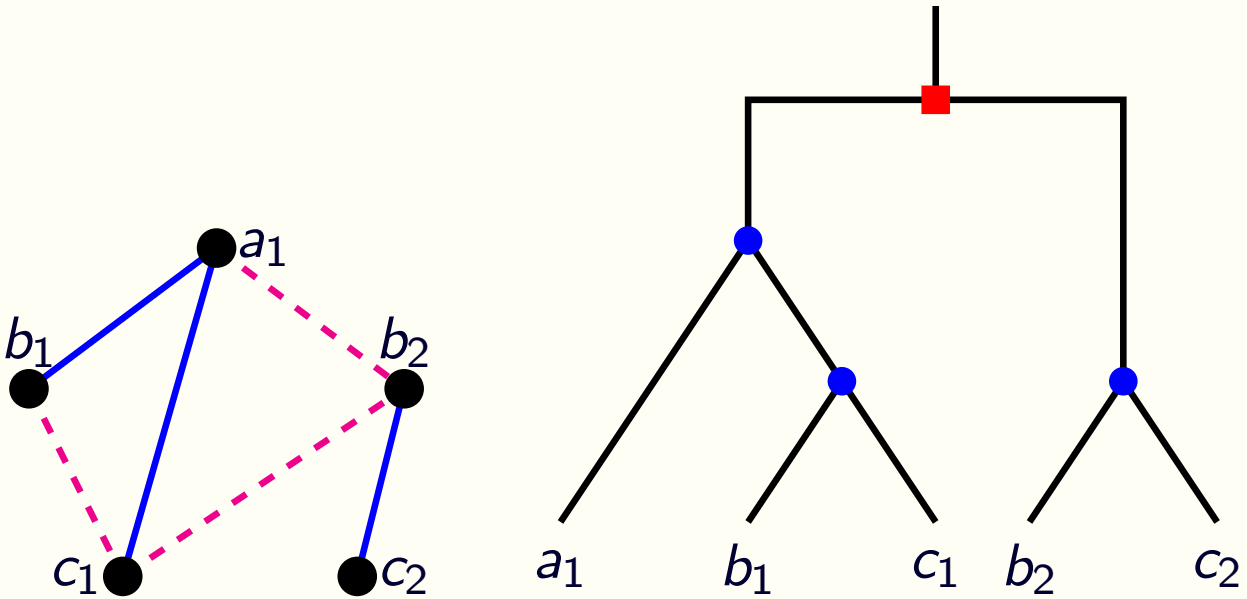

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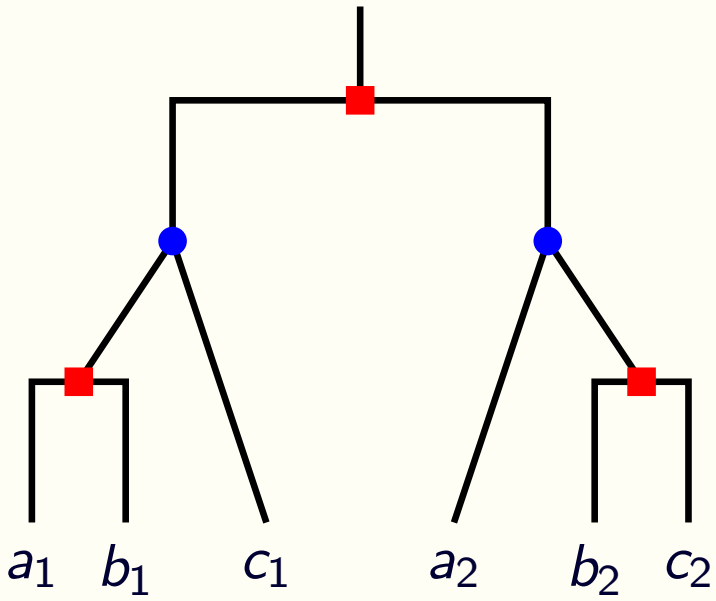

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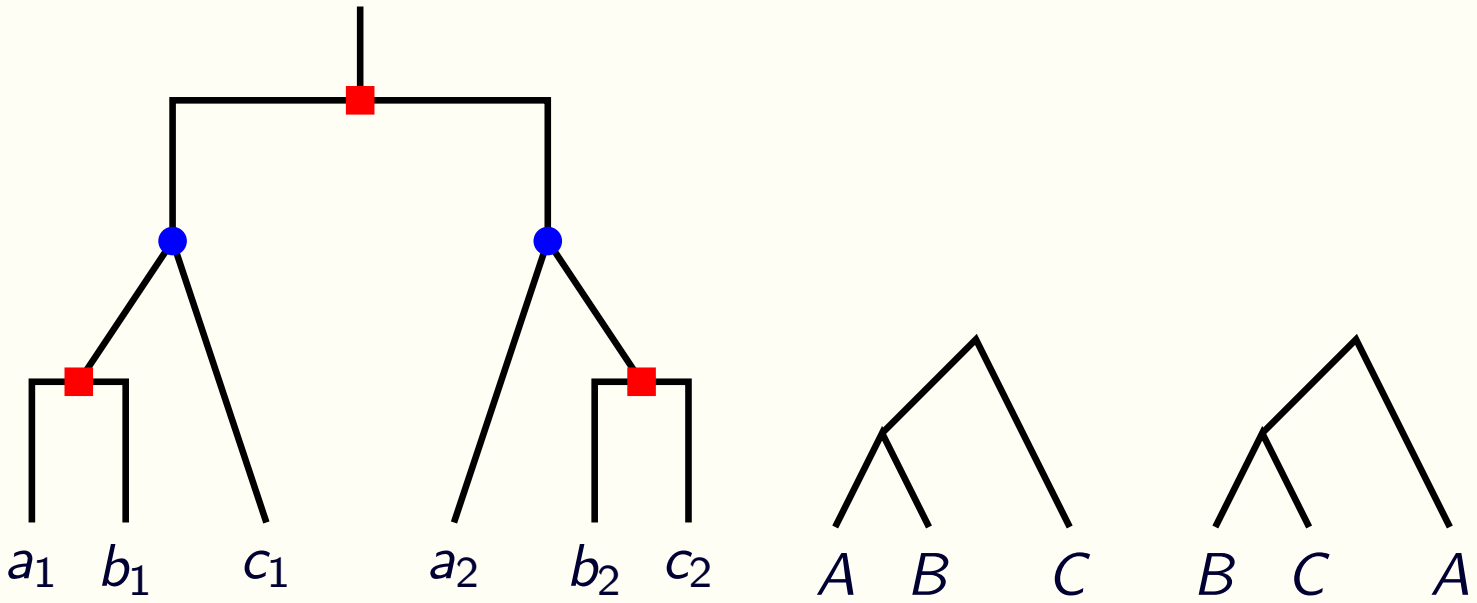

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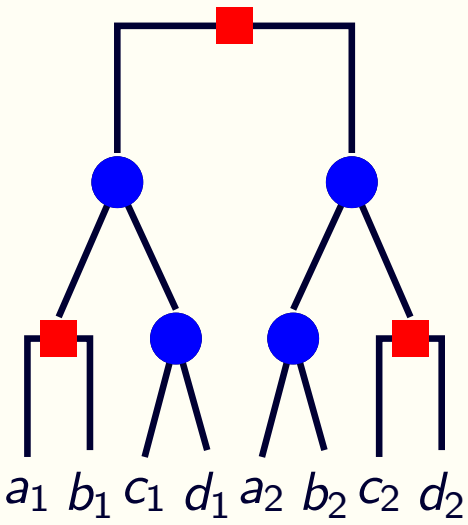
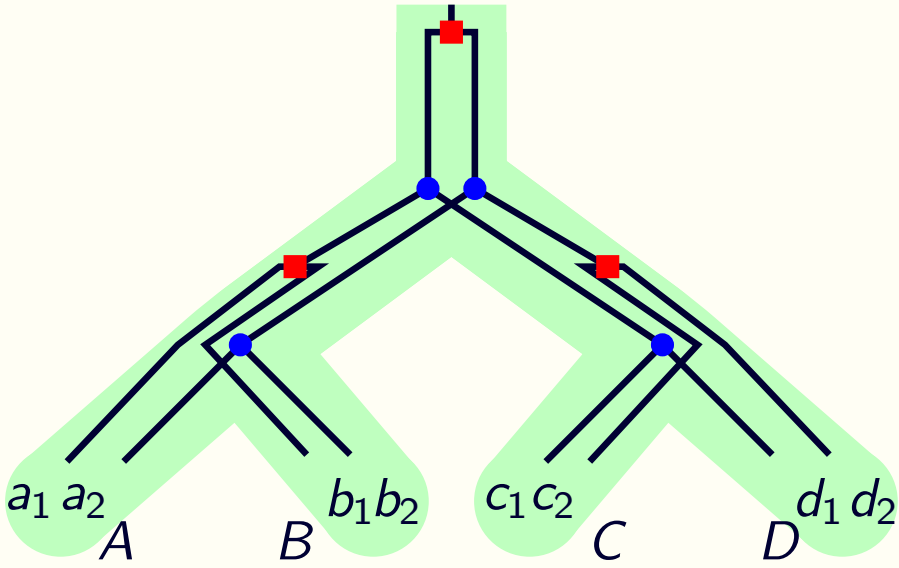
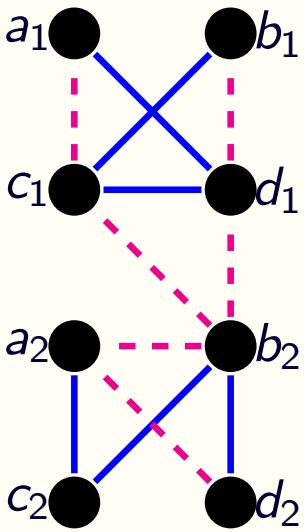
Consistency with a species tree

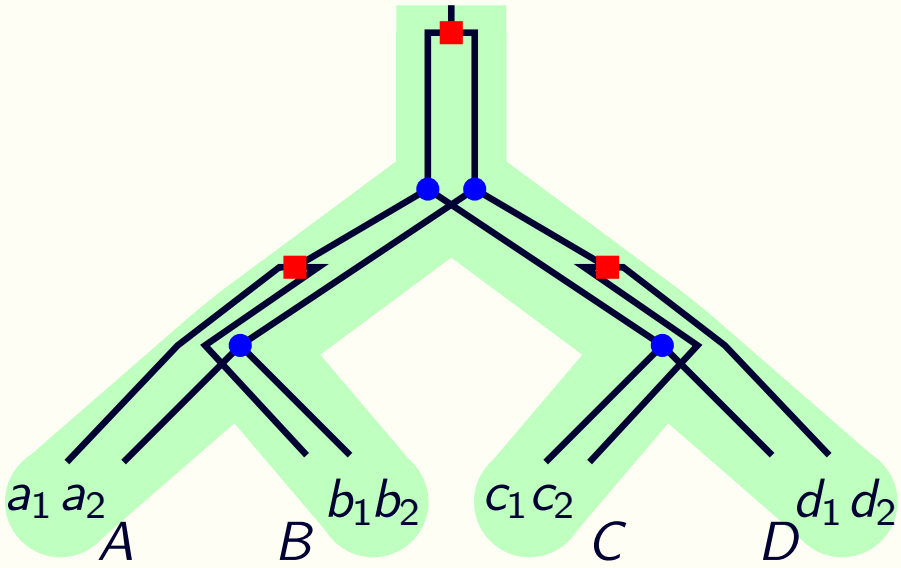




- DS-tree T is **consistent** with species tree S if T can be embedded in S s.t. every speciation coincides with a branching in S, and every gene is mapped to its species.
- More formal (equivalent) definition:
  Given a DS-tree T on V and species assignment $s : V \to \Sigma$, and a species tree S on Σ, T is **consistent** with S if for every speciation event z in T, and distinct children x, y of z, $lca_S(s(leaf_T(x)))$ and $lca_S(s(leaf_T(y)))$ are separated in S.

Problem Definition





- **Input:** A constraint graph $G = (V, E \cup \mathit{Unknown})$ on vertex set V; species mapping $s : V \to \Sigma$
- **Output:** A DS-tree T on V; species tree S on Σ; s.t. T *satisfies* G and is *consistent* with S.

Previous Results

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- Polynomial time algorithm when S is known (Lafond & El-Mabrouk, 2014[2])
- Polynomial tile algorithm when T is known i.e. G has no unknown pairs (using BUILD algorithm[3]).
- **Our result:** Polynomial time algorithm for general case (S and T unknown).

[2] Lafond, M., El-Mabrouk, N.: Orthology and paralogy constraints: satisfiability and consistency. BMC genomics (2014)

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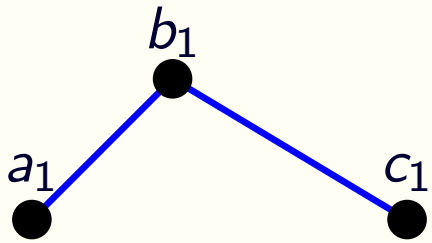
Simple example: three genes



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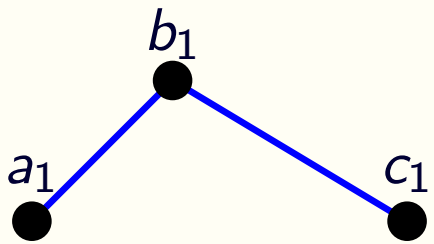

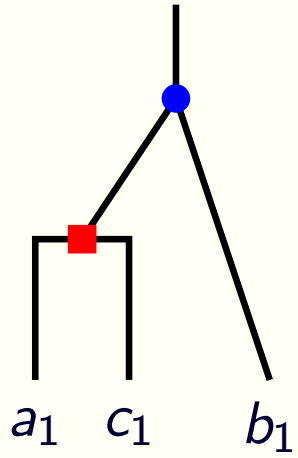

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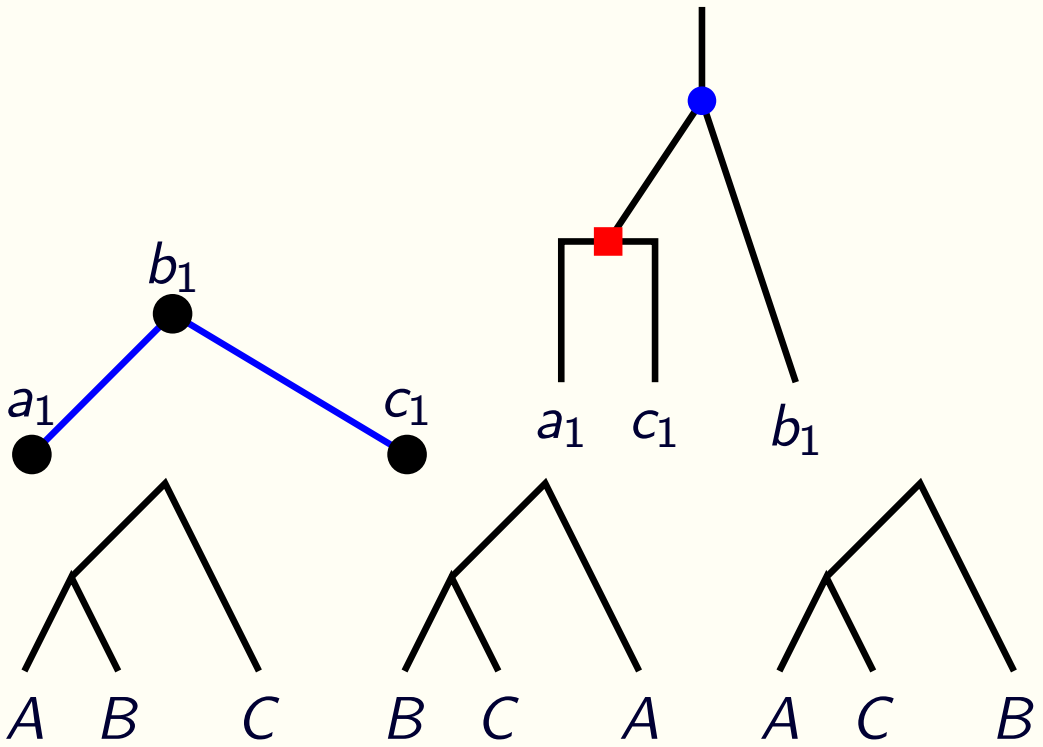

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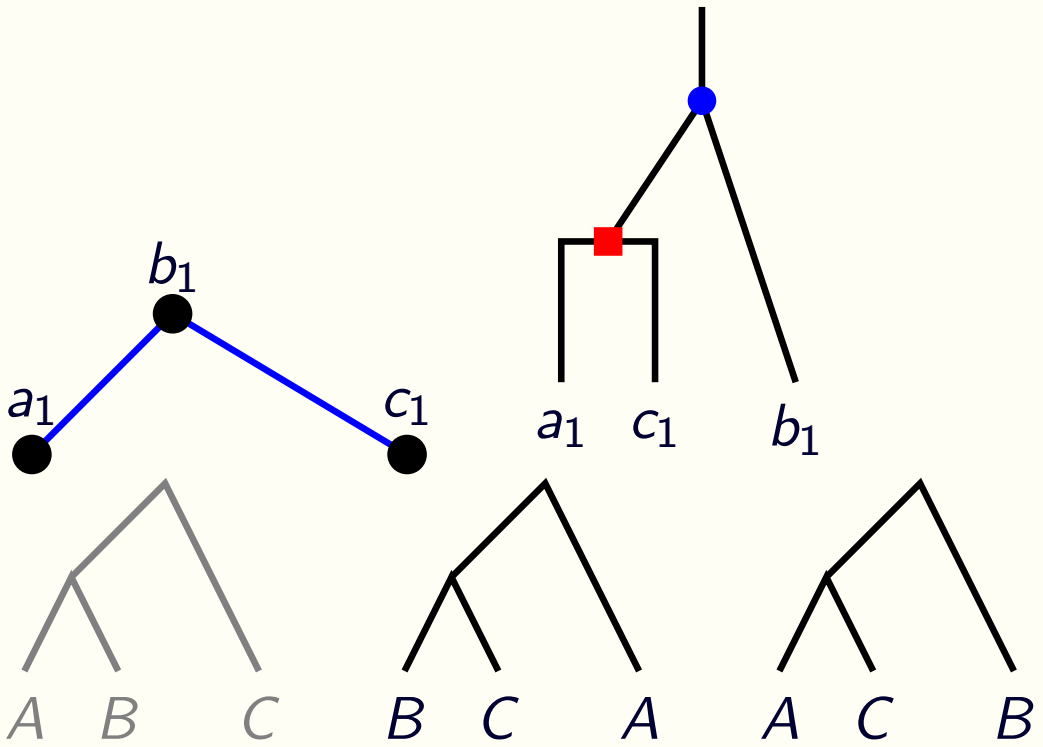

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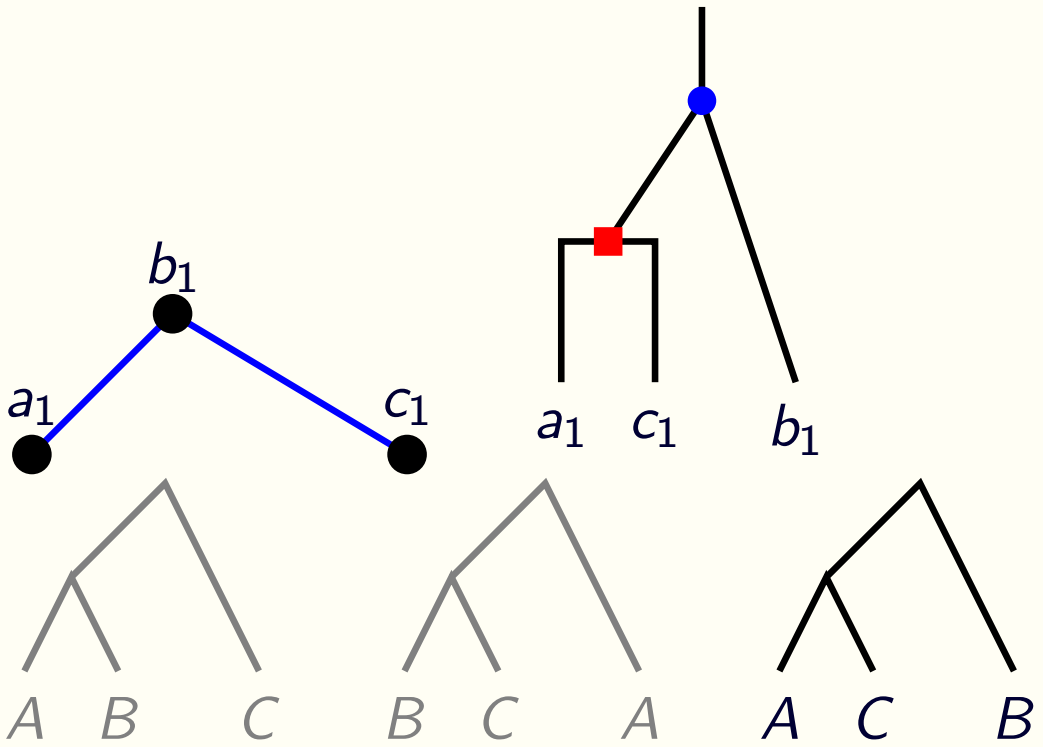

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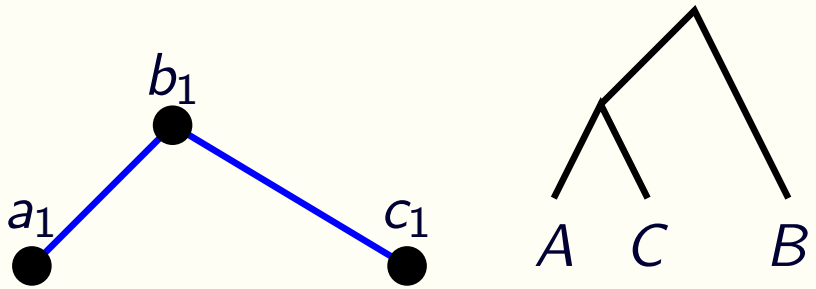

- Given a graph $G = (V, E)$ (no unknown pairs), define $P_3(G) = \{s(x)s(y)|s(z) : xy \in E, yz \in E, xz \notin E\}$.
- For any $AC|B \in P_3(G)$, we must have that $AC|B$ is displayed by the species tree.

Theorem (Lafond & El-Mabrouk, 2014)

Let $G = (V, E)$ have a DS-tree T and let $s : V \to \Sigma$ be a species assignment. Let S be a species tree on Σ. Then T is consistent with S if and only if S displays all triplets in $P_3(G)$.

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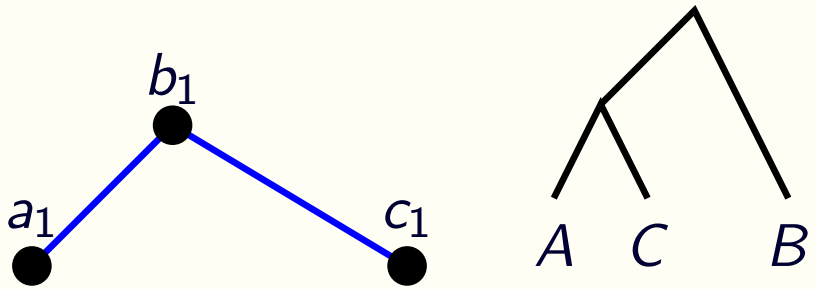

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Consistency dependant on triplets

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- Thus if T is known, we just need an algorithm to determine consistency of a set of triples.
- Such an algorithm exists (BUILD algorithm[4]).

[4] Aho, A.V., Sagiv, Y., Szymanski, T.G., Ullman, J.D.: Inferring a tree from lowest common ancestors with an application to the optimization of relational expressions. SIAM J. Comput. (1981)

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Algorithm when T is known

SpeciesTree($G = (V, E), s : V \to \Sigma$):

1 Set $H = (\Sigma, F = \emptyset)$;
2 **For**$(AC|B \in P_3(G))$:
3 Set $F = F \cup \{AC\}$;
4 **If** H is disconnected:
5 Find partition $\Sigma = X \uplus Y$ such that $X \times Y \cap F = \emptyset$;
6 $root.add\_child$(SpeciesTree($G[s^{-1}(X)], s_X$);
7 $root.add\_child$(SpeciesTree($G[s^{-1}(Y)], s_Y$);
8 **Return** $root$;
9 **Else**:
10 **Return** NULL;

Algorithm when S is known

ConsistentSandwichCograph($G = (V, E \cup \mathit{Unknown}), S, s : V \to V(S)$):

1 **If** $G - \mathit{Unknown}$ is disconnected:
2 Find partition $V = V_1 \uplus V_2$ such that $V_1 \times V_2 \cap E = \emptyset$;
3 Set $\mathit{root}.\mathit{type} = \mathit{Dup}$;
4 **Else**:
5 Find partition $V = V_1 \uplus V_2$ such that $V_1 \times V_2 \subset E \cup \mathit{Unknown}$ and $s(V_1), s(V_2)$ are separated in S;
6 Set $\mathit{root}.\mathit{type} = \mathit{Spec}$;
7 $\mathit{root}.\mathit{add\_child}$(SandwhichCograph($G[V_1]$));
8 $\mathit{root}.\mathit{add\_child}$(SandwhichCograph($G[V_2]$));
9 **Return** root;

Our main result

Theorem

In $O(n^3)$ time, given a constraint graph C on n genes, we can find a DS-tree T satisfying C, and a species S consistent with T (if such S, T exist).

- Proof combines previous algorithms for cases when S known/ T known.
- Can be used to provide evidence for sturcture of a species tree in cases where this is uncertain.

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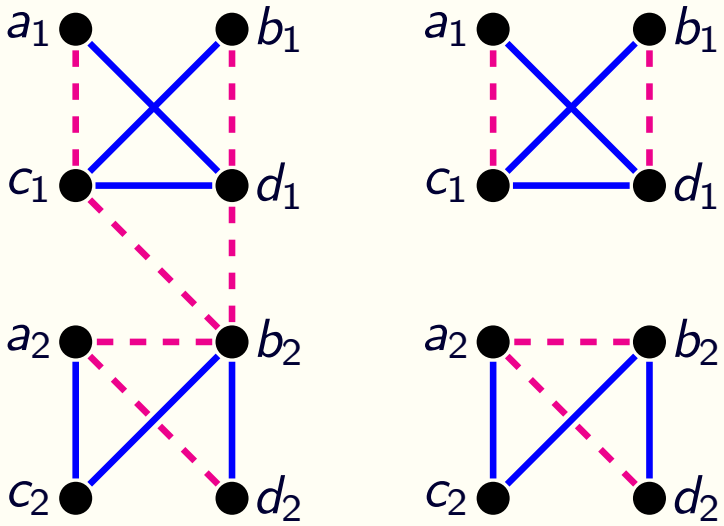
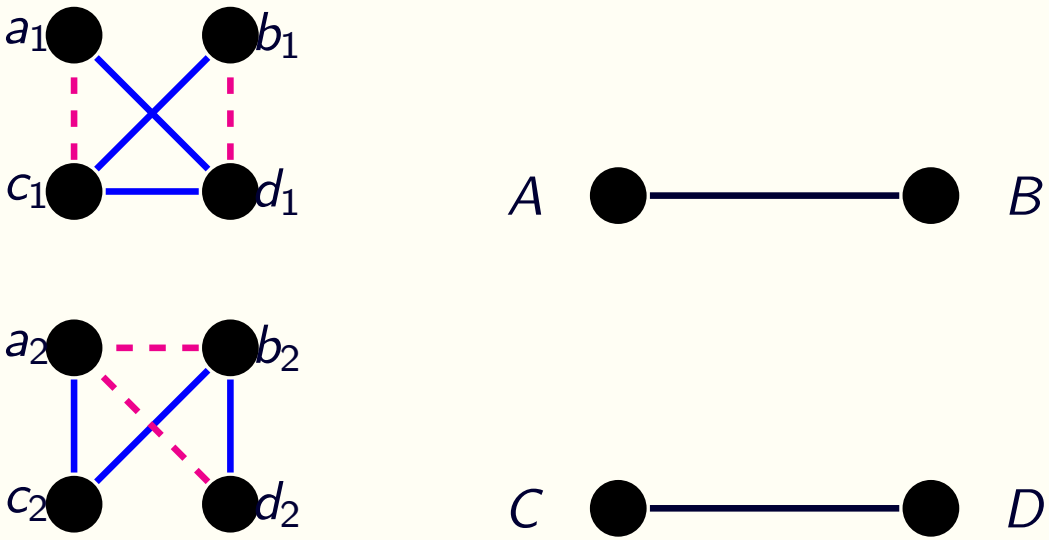
Algorithm Sketch



- Mark as paralog every unknown edge xy such that x and y belong to distinct connected components of known orthologs.

Algorithm Sketch



- Construct a species graph H by connecting A, B iff there exist gene x in species A, y in species B, such that x, y are in the same component of C and xy are known paralogs.
- If H is connected, there is no solution.
- If H can be partitoned into disjoint parts $\mathcal{X}, \mathcal{Y}$, we can assume the first branch of our species tree separates $\mathcal{X}$ and $\mathcal{Y}$

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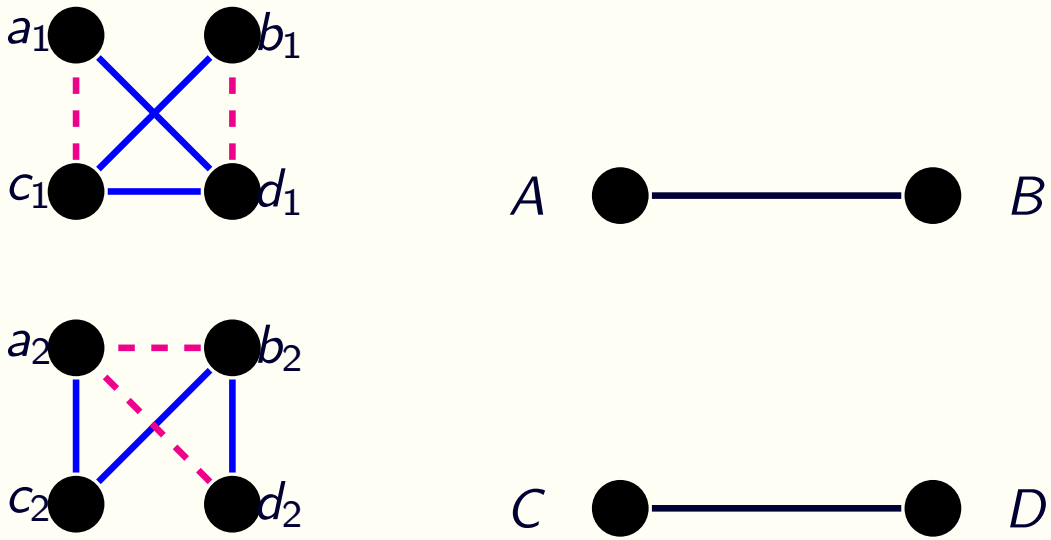

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Our Algorithm

ConsistentSandwichCograph($G = (V, E \cup \mathit{Unknown}), s : V \to \Sigma$):

1 **If** $G - \mathit{Unknown}$ is disconnected:
2 Delete edges in *Unknown* between components of $G[E]$;
3 **For**$(x, z \in V)$:
4 **If**$(x, z$ in same componet of $G[E]$ but $xy \notin E \cup \mathit{Unknown})$:
5 Add $s(x)s(z)$ as an edge in H;
6 **If** $H = (F, \Sigma)$ is disconnected:
7 Find partition $\Sigma = X \uplus Y$ such that $X \times Y \cap F = \emptyset$;
8 $\mathit{root}.\mathit{add\_child}(\text{SpeciesTree}(G[s^{-1}(X)], s_X)$;
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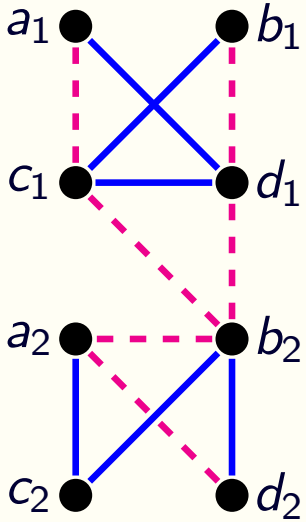
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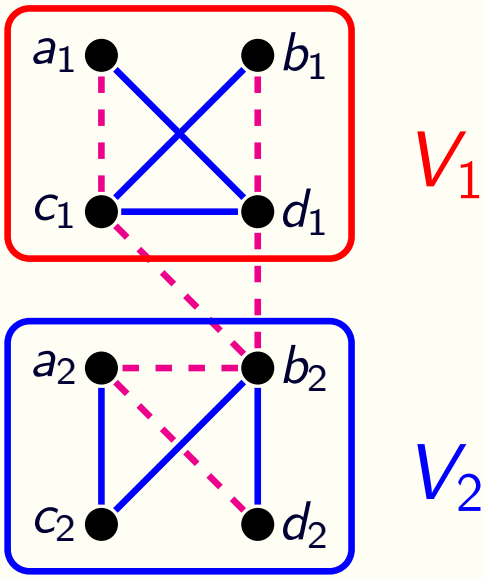
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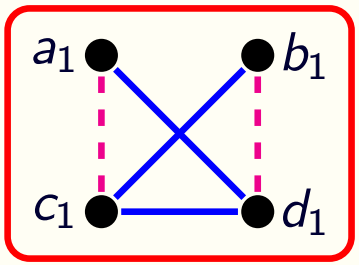
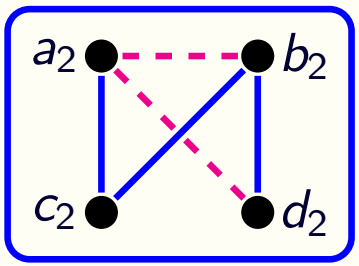
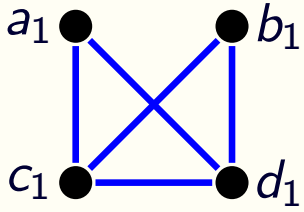
V_2



V_1



V_2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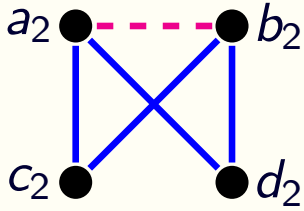
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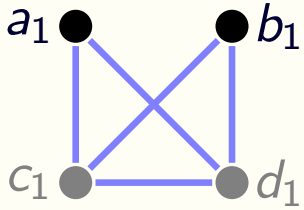
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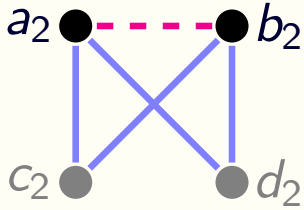
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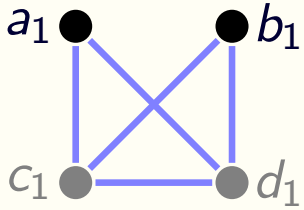
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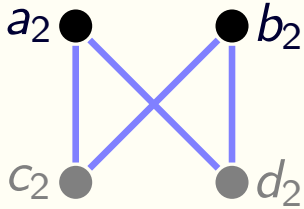
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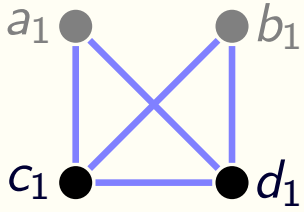
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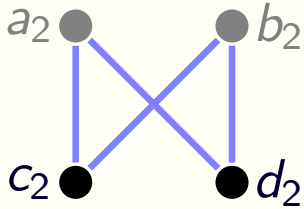
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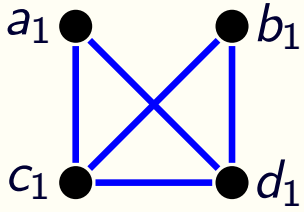
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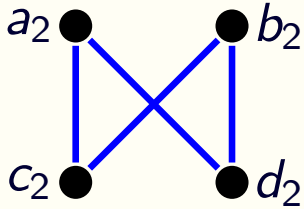
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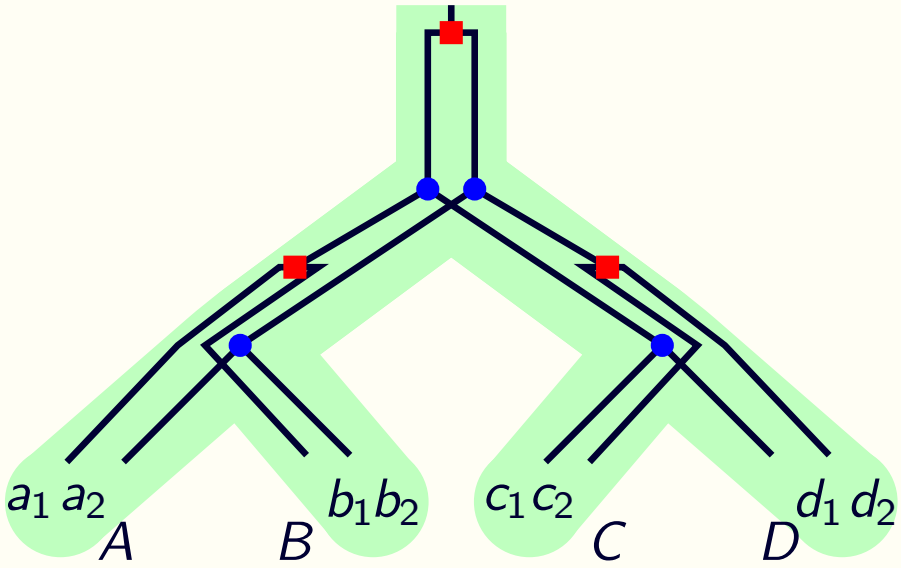

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Minimizing Duplications

Input: A constraint graph C on vertex set V; species mapping $s : V \to \Sigma$

Output: A DS-tree T on V; species tree S on Σ; s.t. T *satisfies* C and is *consistent* with S and T has *minium* number of duplication events.

- This problem is NP-hard (reduction from graph coloring).
- NP-hard even to decide if 2 duplications is possible.
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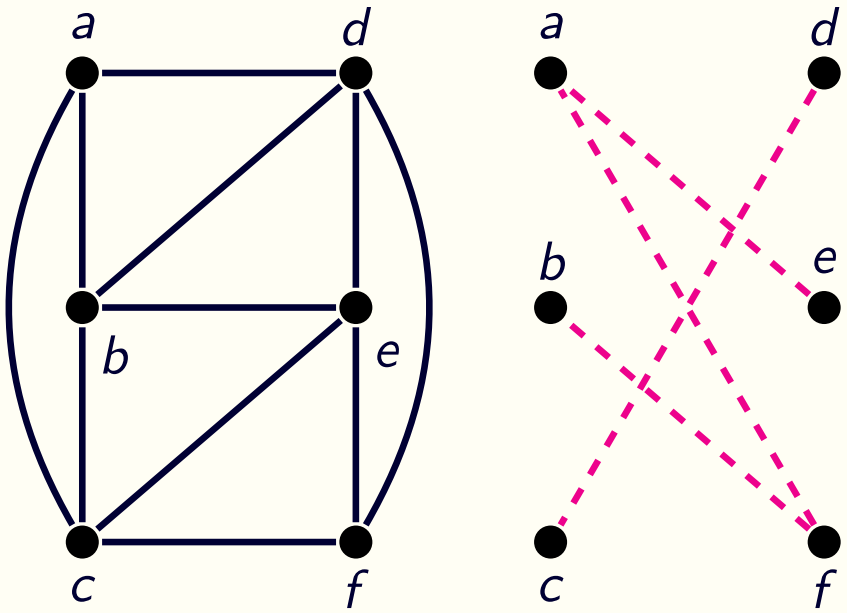
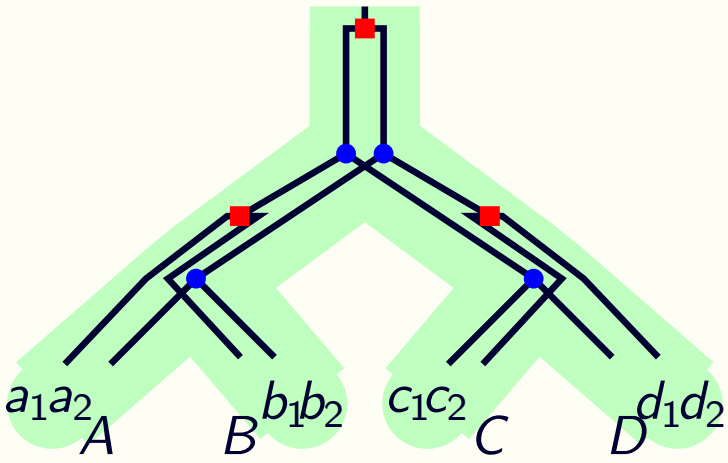
Reduction from graph coloring



- Given a graph $H = (V, F)$, let constraint graph $G = (V, E \cup \mathit{Unknown})$, $E = \emptyset$, $\mathit{Unknown} = \bar{F}$. Then H is $k+1$-colorable iff G has a DS-tree T with at most k duplications.

Extending to transfer networks



- We have been assuming that all gene propagation occurs in a species **tree**.
- In practice, **lateral gene transfer** can occur between branches.
- Open questions: Can we solve satisfy constraint graphs if the DS-tree must be "embedded" in an **acyclic network**

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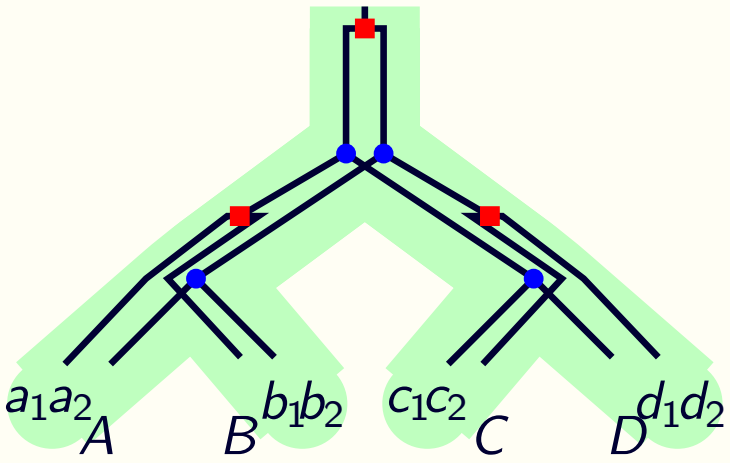

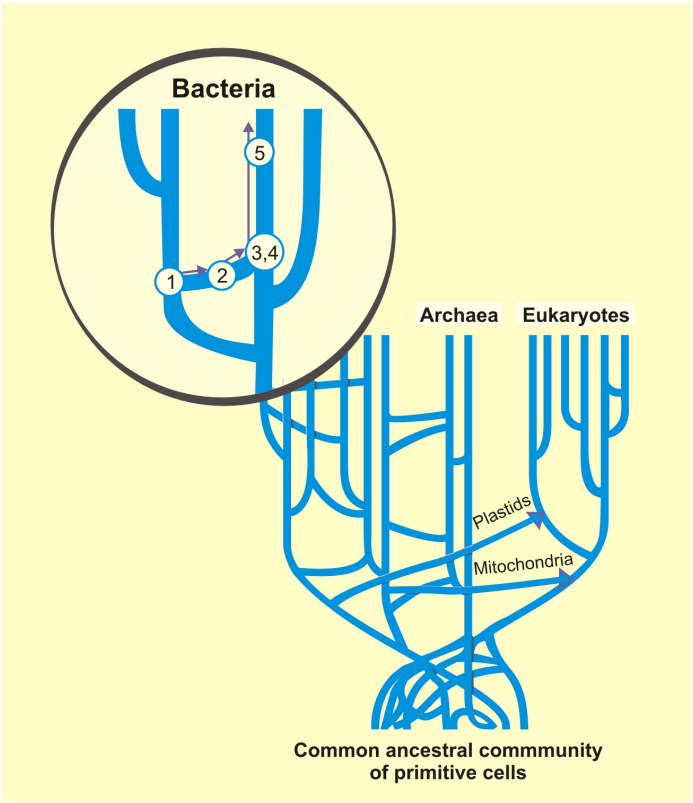

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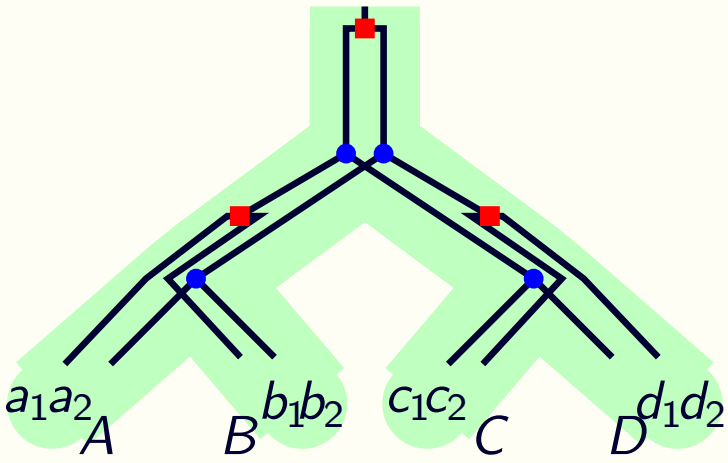

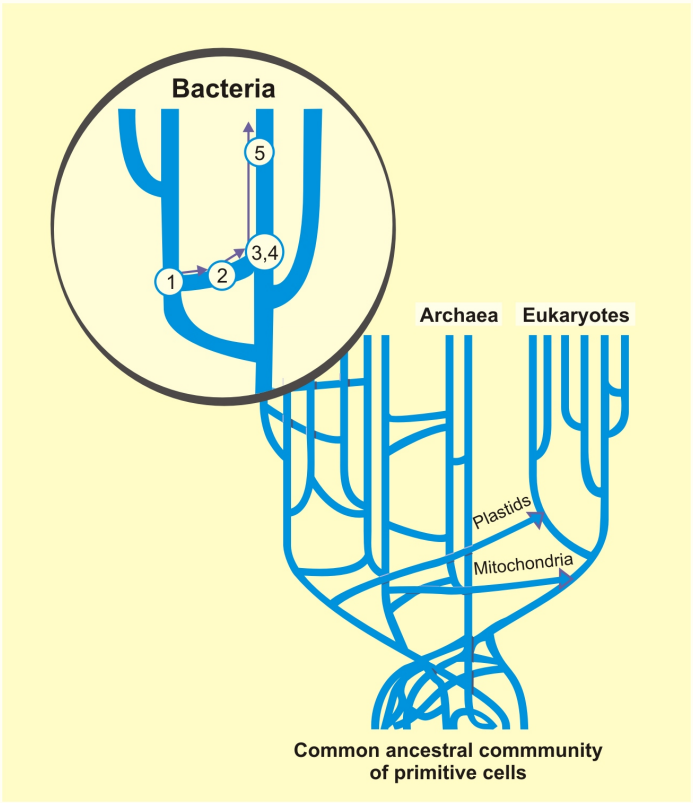

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Experiments: Test instances

- Generated a set of connstraint graphs using data from ensembl.org.
- Chose 265 gene families of vertebrates with more than 20 genes from *Ensembl*.
- For each family, ProteinOrtho was ran to generate orthology relation graphs.
- By running ProteinOrtho with two different parameter settings (stricter vs looser characterization of orthology), a constraint graph is derived. (Unknown edges = edges marked as orthologs under one parameter and paralogs under another).
- (Same data set as used by Lafond & El-Mabrouk.)

Experiments: Test instances

- We ran our algorithm on the generated test instances.
- The hope: species trees returned by our algorithm could be reconciled to produce the known species tree.
- Unfortunately this was not the case :(
- DS-trees and species trees returned by our algorithm were very "flat", difficult to combine into a full picture.
- We believe this is partially due to small data size; hope to do better on a larger data set.

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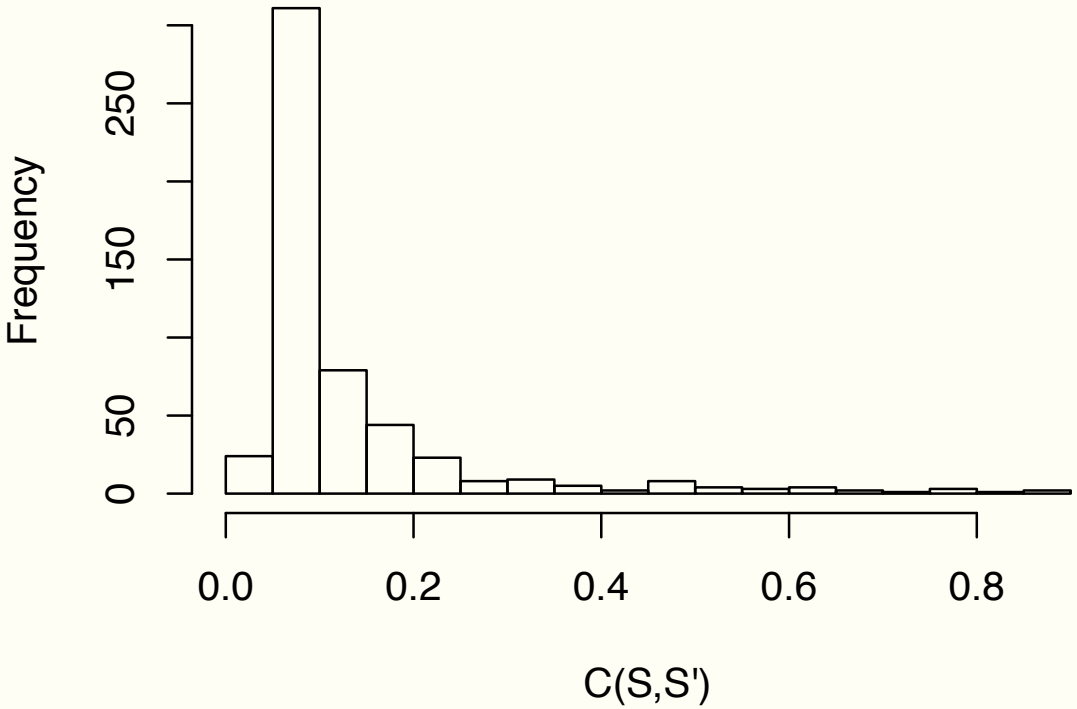
Relative consistency withknown species tree



- Of the satisfiable constraint graphs, 534 out of 2385 were not consistent with known species tree S.
- For 533 of these, our algorithm found a species tree S' for which they *were* consistent.
- We estimated the discordancy between S and each S' by finding minimum of triplets of S that must be unsatisfied in a tree not contradicting S'.

Future Work

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- Apply algorithm on larger data sets.
- Extend algorithm to account for gene transfers (currently being worked on...).
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Thanks for listening!

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