Lecture: Graph-Based Genome Scaffolding

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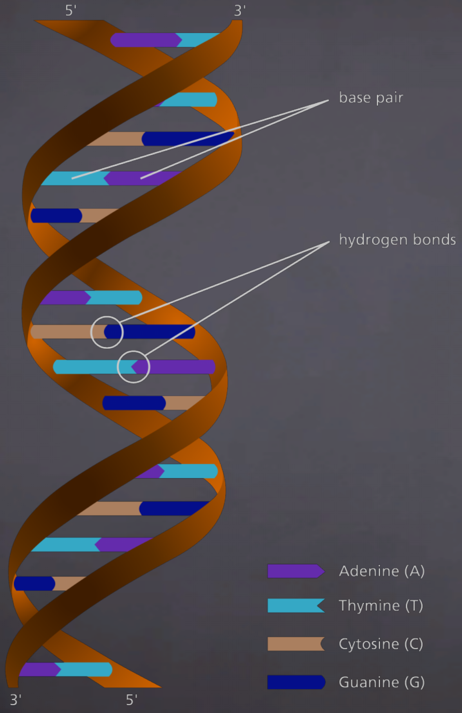
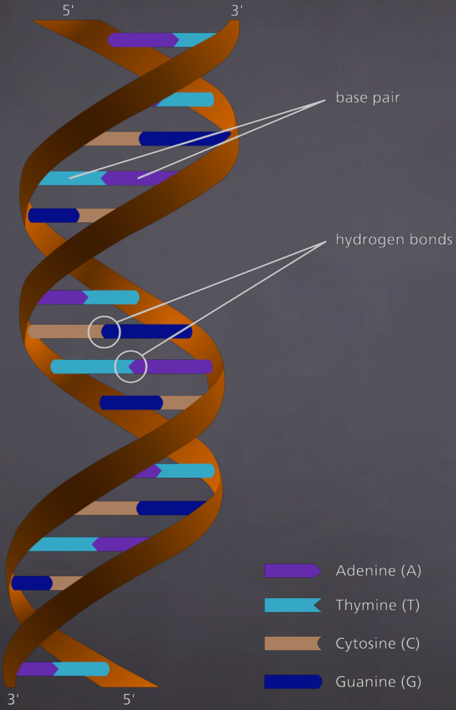


DNA

- double strand
- inside nucleus (safe)

RNA

- single strand
- outside nucleus
- transfers genetic code
- Thymine (T) → Uracil (U)



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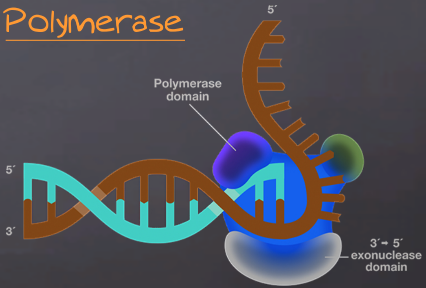
Polymerase



Sanger Sequencing

[Sanger et al '77]

```
CCTGGACGGGTCAGACATGACAGTGGCCCCAAGATTCACAAGATCGTATCTCAATACAGTAAACGAGCAAT
GGACCTGCCCAGTCTGTACTGTCACCGGGGTTCTAAGTGTTCTAGCATAGAGTTATGTCATTTGCTCGTTA
```

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Sanger Sequencing

1. split helix & create thousands of copies

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2. add polymerase & floating bases: A C G T
3. add a special base: A* (polymerase cannot extend)

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   ⇝ each length is the position of a T in the template

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Problem

unreliable after a couple hundred bp
⇝ chop up DNA into pieces and read those

Next Generation Sequencing (illumina)

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ACTCA......ACCTC

1. chop DNA into smaller pieces

Next Generation Sequencing (illumina)

TGGTACTCA......ACCTCTCAG

1. chop DNA into smaller pieces
2. add anchors to each end of each piece

Next Generation Sequencing (illumina)

TGGTACTCA......ACCTCTCAG

1. chop DNA into smaller pieces
2. add anchors to each end of each piece
3. "flow cell" containing anchor places

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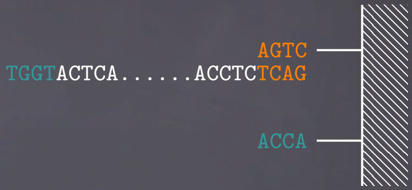

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4. strand anchors its two ends to two anchor places

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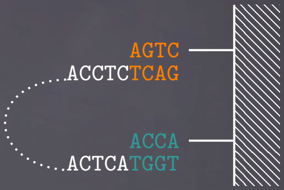

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5. polymerase completes the strand into double-strand

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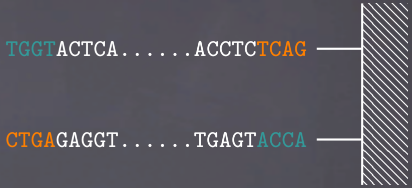

1. chop DNA into smaller pieces
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6. double strand is denaturized into single strands

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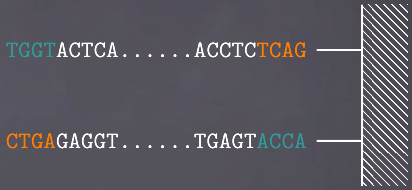

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7. rinse, repeat (last 3 steps) until flow chip is "full"

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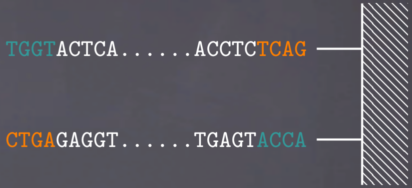

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8. read all strands from their anchor points outwards

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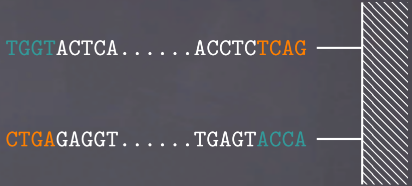

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8. read all strands from their anchor points outwards

⇝ Paired-End reads (distance between reads = "insert size")

Sequence Assembly: Overview

GCCCCTGAACTTCGCTAGGGTTCTCTAACGACACTCCTTGGGTTTTTACGTCGCGGTTCTCTAGGCCATTGATTGCGGGTCCAGGTGCTGTCAACGAC

Goal: reconstruct sequence

Idea: overlap reads

Sequence Assembly: Overview

```
GCCCCTGAACTTCGCTAGGGTTCTCTAACGACACTCCTTGGGTTTTTACGTCGCGGTTCTCTAGGCCATTGATTGCGGGTCCAGGTGCTGTCAACGAC
GCCCCTGAACTT                            CGACACTCCTTGGGTTTT                  CTAGGCCATTGATTGCGGGTC
          ACTTCGC                                                   GGTTCTCT                 GGTCCAGGTGCTGTCAACGAC
```

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GCCCCTGAACTT                CGACACTCCTTGGGTTTT             CTAGGCCATTGATTGCGGGTC
        ACTTCGC                                      GGTTCTCT               GGTCCAGGTGCTGTCAACGAC
GCCCCTGAACTTCGC             CGACACTCCTTGGGTTTT       GGTTCTCTAGGCCATTGATTGCGGGTCCAGGTGCTGTCAACGAC
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GCCCCTGAACTT                CGACACTCCTTGGGTTTT              CTAGGCCATTGATTGCGGGTC
        ACTTCGC                                       GGTTCTCT               GGTCCAGGTGCTGTCAACGAC
GCCCCTGAACTTCGC             CGACACTCCTTGGGTTTT        GGTTCTCTAGGCCATTGATTGCGGGTCCAGGTGCTGTCAACGAC
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Problem 1: parts of the sequence might not be covered by reads

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GCCCCTGAACTT                   CGACACTCCTTGGGTTTT                CTAGGCCATTGATTGCGGGTC
        ACTTCGC                                              GGTTCTCT                  GGTCCAGGTGCTGTCAACGAC
           TCGCTAGGGTTCTCTAACGA                        TTTACGTCGCGG                                     CGAC
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Problem 1: parts of the sequence might not be covered by reads
$\rightsquigarrow$ sequence with "high coverage"

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ACTTCGC GGTTCTCT GGTCCAGGTGCTGTCAACGAC

TCGCTAGGGTTCTCTAACGA TTTACGTCGCGG CGAC

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        ACTTCGC                                       GGTTCTCT               GGTCCAGGTGCTGTCAACGAC
           TCGCTAGGGTTCTCTAACGA             TTTACGTCGCGG                                      CGAC
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Problem 2: Shortest Common Superstring is NP-hard
$\rightsquigarrow$ "Overlap-Layout-Consensus" assemblers

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GCCCCTGAACTTCGCTAGGGTTCTCTAACGACACTCCTTGGGTTTTACGTCGCGGTTCTCTAGGCCATTGATTGCGGGTCCAGGTGCTGTCAACGAC
GCCCCTGAACTT                CGACACTCCTTGGGTTTT                CTAGGCCATTGATTGCGGGTC
        ACTTCGC                                    GGTTCTCT                      GGTCCAGGTGCTGTCAACGAC
           TCGCTAGGGTTCTCTAACGA              TTTACGTCGCGG                                          CGAC
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Problem 2: Shortest Common Superstring is NP-hard
⇝ "Overlap-Layout-Consensus" assemblers
1. produce best pairwise overlaps
2. layout the reads according to the overlaps
3. for each position, compute consensus base

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GCCCCTGAACTC                CGACACTCCTTGGGTTTT             CTAGGCCATTGATTGCGGGTC
       ACTTCGC                                         GGTTCTCT                 GGTCCAGGTGCTGTCAACGAC
          TCGCTAGGGTTCTCTAACGA                TTTACGTCGCGG                                        CGAC
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        ACTTCGC                                          GGTTCTCT                 GGTCCAGGTGCTGTCAACGAC
           TCGCTAGGGTTCTCTAACGA                TTTACGTCGCGG                                     CGAC
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Problem 2: Shortest Common Superstring is NP-hard
$\rightsquigarrow$ "Overlap-Layout-Consensus" assemblers
Problem: $\Theta(n^2)$ too slow in practice
$\rightsquigarrow$ DeBruijn-graph based assembly

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GCCCTGAACTT              CGACACTCCTTGGGTTTT              CTAGGCCATTGATTGCGGGTC
      ACTTCGC                                     GGTTCTCT                GGTCCAGGTGCTGTCAACGAC
         TCGCTAGGTTCTCTAACGA            TTTACGTCGCGG                                       CGAC
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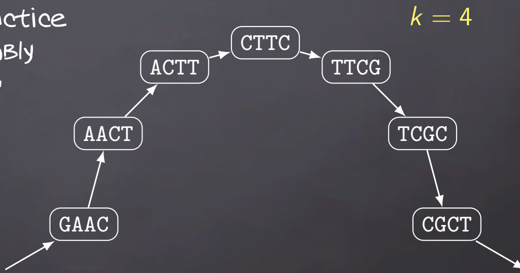
⇝ DeBruijn-graph based assembly

1. chop all reads into "k-mers"
2. builds overlap graph ("DeBruijn graph")
3. find path using all overlaps



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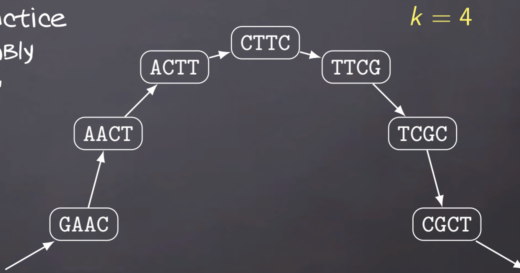

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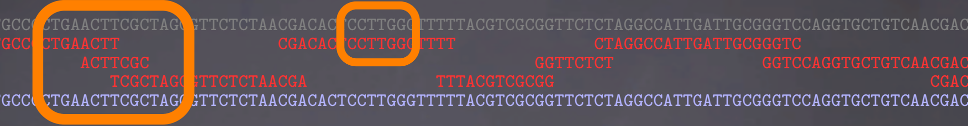

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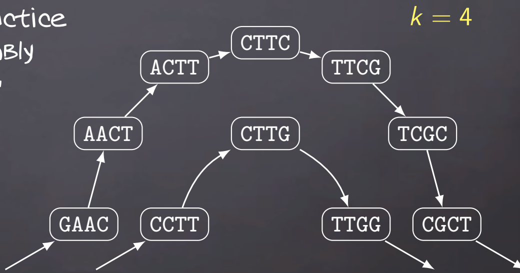

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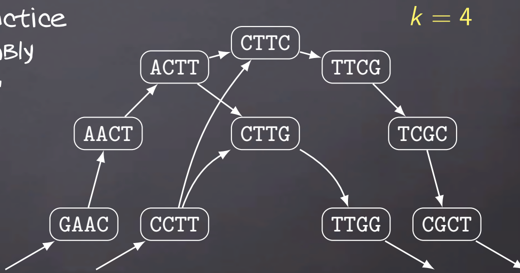

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       ACTTCGC                                        GGTTCTCT                 GGTCCAGGTGCTGTCAACGAC
          TCGCTAGGGTTCTCTAACGA              TTTACGTCGCGG                                        CGAC
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Problem 3: repeats (common in DNA) make assembly ambiguous

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ACTTCGC GGTTCTCT GGTCCAGGTGCTGTCAACGAC

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        ACTTCGC   GGTTCTCT                                                   GGTCCAGGTGCTGTCAACGAC
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        ACTTCGC    GGTTCTCT                                                     GGTCCAGGTGCTGTCAACGAC
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Problem: "contig soup" not very useful

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But: we have paired-end information!

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        ACTTCGC   GGTTCTCT                                                           GGTCCAGGTGCTGTCAACGAC
           TCGCTAGGGTTCTCTAACGA             TTTACGTCGCGG                                               CGAC
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Genome Scaffolding: Previous Work

Goal: order & orient contigs
Idea: use pairing information on reads to "link" contigs together

- SOPRA [Dayarian, Michael, Sengupta, BMC Bioinf. 11, '10]
  - removes reads in high-coverage area (likely repeats)
  - orientation step (heuristic) + ordering step (heuristic)
  - coded in Pearl (!!!)
  - (observed sparse contig graph)

Genome Scaffolding: Previous Work

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- SOPRA [Dayarian, Michael, Sengupta, BMC Bioinf. 11, '10]
- SSPACE [Boetzer & al., Bioinf. 27(4), '11]
  - heuristic contig extension
  - "reasonable time"

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- SSPACE [Boetzer & al., Bioinf. 27(4), '11]
- OPERA [Gao, Sung, Ngaraja, JCB. 18(11), '11]
  - $n^{p+O(1)}$ time ($p =$#edge-deletions ($\geq$ feedback edge set))
  - most work done by a heuristic "graph contraction"

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- GRASS [Gritsenko & al., Bioinf. 28(11), '12]
  - Mixed-Integer Quadratic Programming
  - deals with uncertain data (slack variables)

    ⇝ "intractable even for small # of contigs"
  - heuristic workaround:
    - solve relaxed formulation & use slack values ⇝ ILP

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- SSPACE [Boetzer & al., Bioinf. 27(4), '11]
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- GRASS [Gritsenko & al., Bioinf. 28(11), '12]
- SCARPA [Donmez, Brudno, Bioinf. 29(4), '13]
  - orientation step: use FPT algo for Odd Cycle Transversal
  - ordering step: heuristic

Genome Scaffolding: Previous Work

Goal: order & orient contigs
Idea: use pairing information on reads to "link" contigs together

- SOPRA [Dayarian, Michael, Sengupta, BMC Bioinf. 11, '10]
- SSPACE [Boetzer & al., Bioinf. 27(4), '11]
- OPERA [Gao, Sung, Ngaraja, JCB. 18(11), '11]
- GRASS [Gritsenko & al., Bioinf. 28(11), '12]
- SCARPA [Donmez, Brudno, Bioinf. 29(4), '13]
- ... [Huson & al., JACM, '02][Nieuwerburgh & al., NAR, '12]

Graph-Based Scaffolding

AACGACACTCCTTGGGTTTTTACGTCGCGG

GTTAATGTCCGAGCATAAAACTCTGGTTGGC

GTACTGAACTTGGGTTCCATAGGACCCAGA

CTAGGCCATTGATTGCGGGTCCAGGTGCTG

AGAGCTTGACAGTAACACATTTAGGAGCACGCG

Graph-Based Scaffolding

GTTAATGTCCGAGCATAAAACTCTGGTTGGC

AACGACACTCCTTGGGTTTTTACGTCGCGG

GTACTGAACTTGGGTTCCATAGGACCCAGA

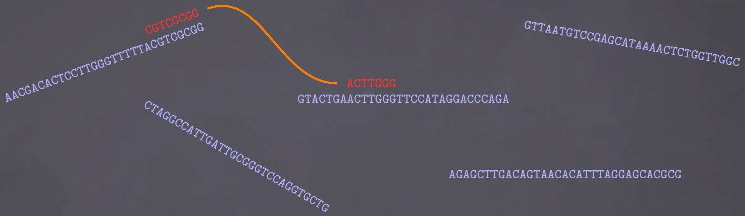
CTAGGCCATTGATTGCGGGTCCAGGTGCTG

AGAGCTTGACAGTAACACATTTAGGAGCACGCG

Strategy

1. map reads into contigs

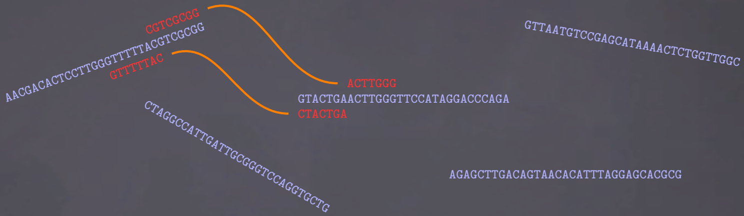
Graph-Based Scaffolding



Strategy

1. map reads into contigs

Graph-Based Scaffolding



Strategy

1. map reads into contigs

Graph-Based Scaffolding

AACGACACTCCTTGGGTTTTTACGTCGCGG

GTTAATGTCCGAGCATAAAACTCTGGTTGGC

CTAGGCCATTGATTGCGGGTCCAGGTGCTG

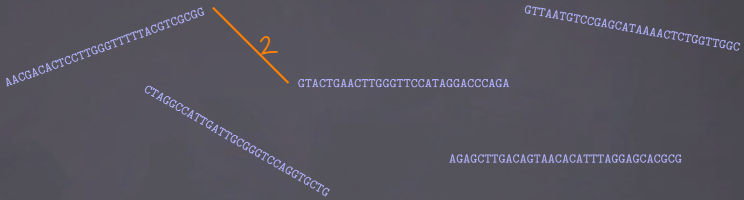
GTACTGAACTTGGGTTCCATAGGACCCAGA

AGAGCTTGACAGTAACACATTTAGGAGCACGCG

Strategy

1. map reads into contigs
2. pair contigs according to read-pairing (weighted)

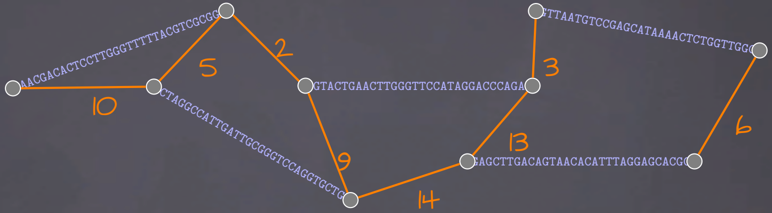
Graph-Based Scaffolding



Strategy

1. map reads into contigs
2. pair contigs according to read-pairing (weighted)

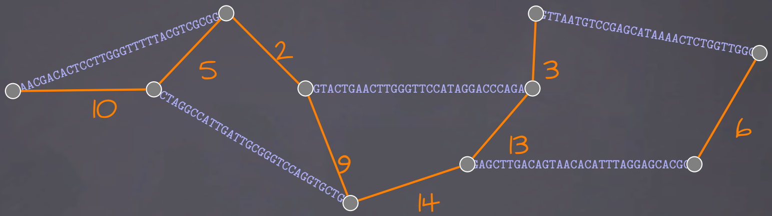
Graph-Based Scaffolding



Strategy

1. map reads into contigs
2. pair contigs according to read-pairing (weighted)

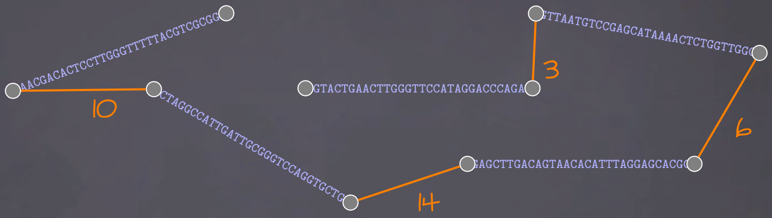
Graph-Based Scaffolding



Strategy

1. map reads into contigs
2. pair contigs according to read-pairing (weighted)
3. cover "scaffold graph" with (heavy) alternating paths
   each path corresponds to a chromosome

Graph-Based Scaffolding



Strategy

1. map reads into contigs
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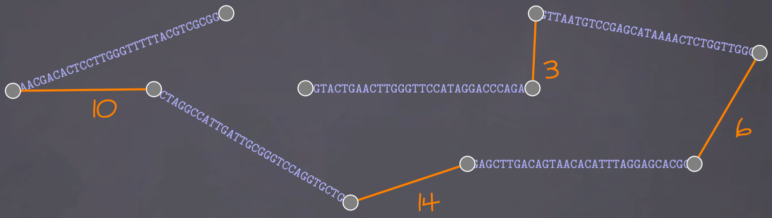
Graph-Based Scaffolding

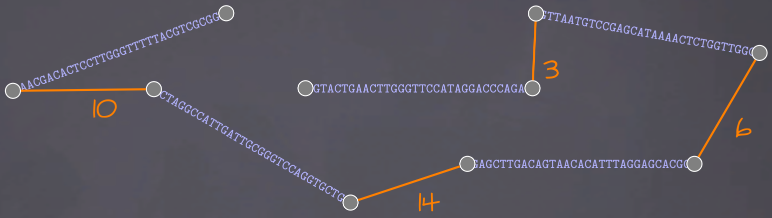


Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths of total weight $\geq k$?

Graph-Based Scaffolding



Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

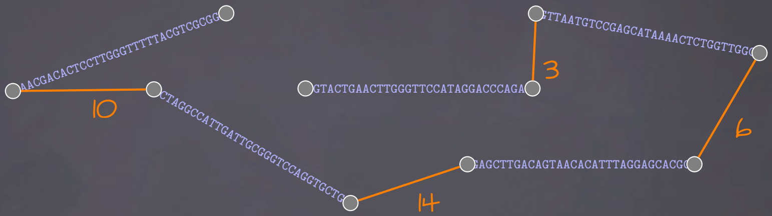
Question: Can G be covered by

$\leq \sigma_p$ alternating paths &

$\leq \sigma_c$ alternating cycles

of total weight $\geq k$?

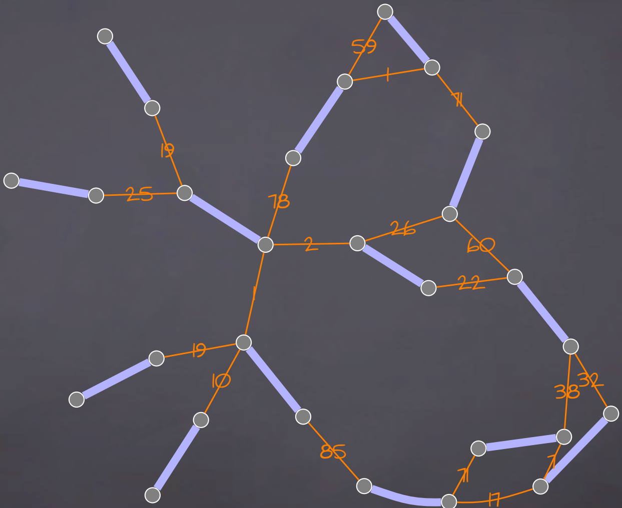
Graph-Based Scaffolding



Exact Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by
σ_p alternating paths &
σ_c alternating cycles
of total weight $\geq k$?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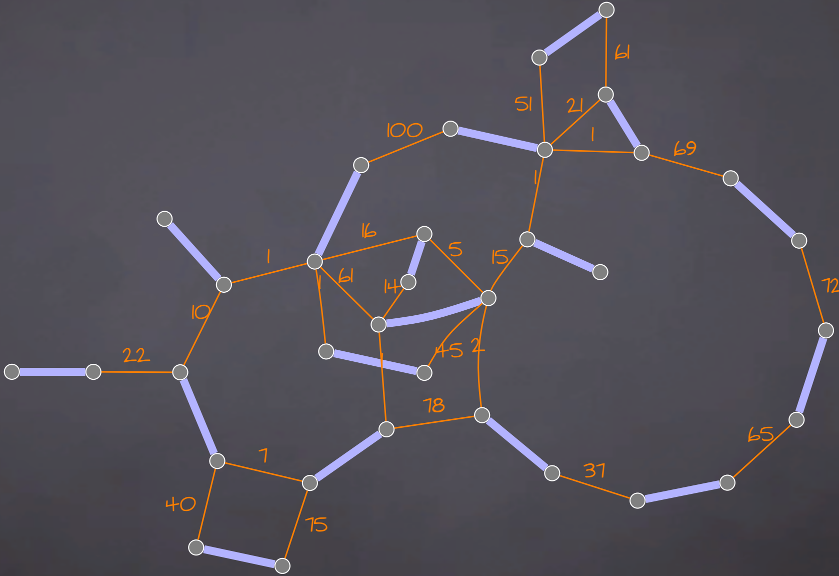
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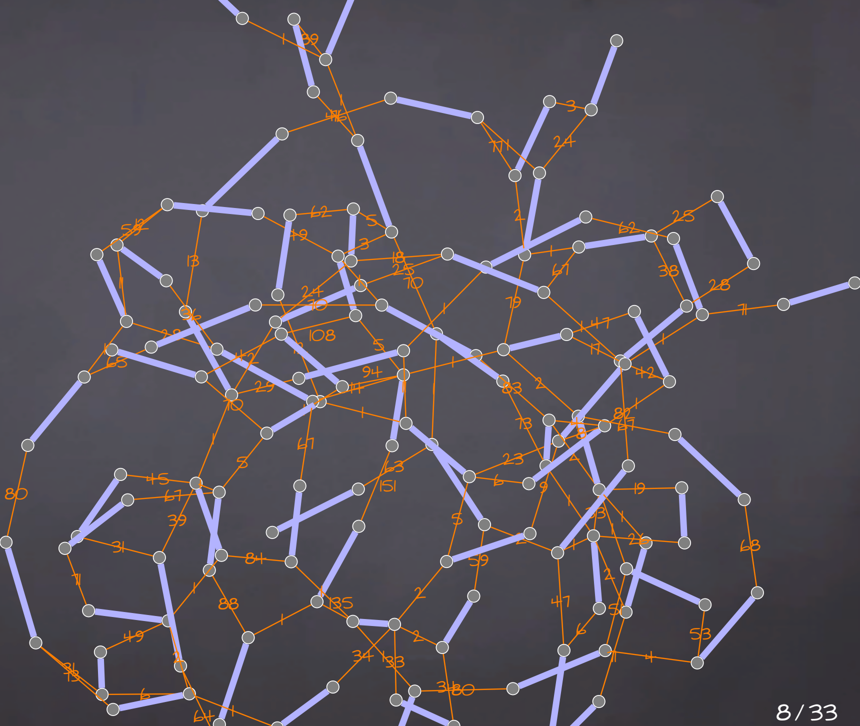

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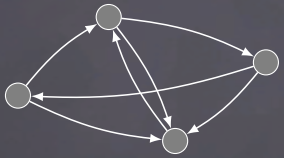
2
59
84
88
135
2
47
6
53
49
6
64
34
33
80
80

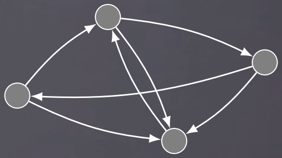
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Construction

Given a directed graph D.

1. make a copy of D

Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?

Construction

Given a directed graph D.

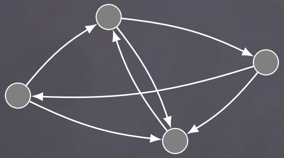
1. make a copy of D
2. duplicate all vertices $\rightsquigarrow M$

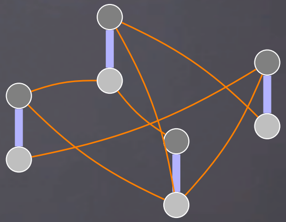
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Construction

Given a directed graph D.

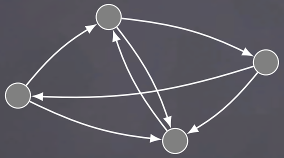
1. make a copy of D
2. duplicate all vertices $\rightsquigarrow M$
3. "slide" down all arrow tips & ignore directions

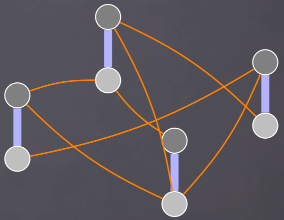
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Lemma

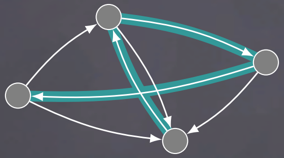
D admits a directed Hamiltonian path $\Leftrightarrow$ M can be covered with a single alternating path in G.

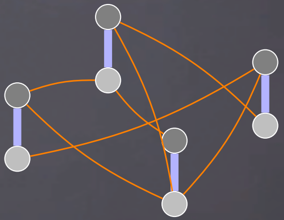
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Lemma

D admits a directed Hamiltonian path $\Leftrightarrow$ M can be covered with a single alternating path in G.

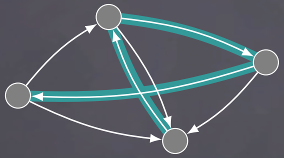
"$\Rightarrow$": replace each v in the Hamiltonian path by $v_{up} \to v_{low}$.

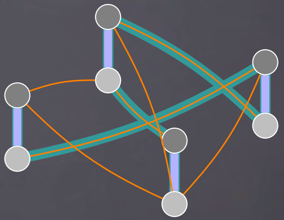
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Lemma

D admits a directed Hamiltonian path $\Leftrightarrow$ M can be covered with a single alternating path in G.

"$\Rightarrow$": replace each v in the Hamiltonian path by $v_{up} \to v_{low}$.

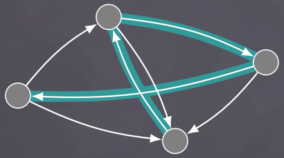
alternating ✓ covers M ✓

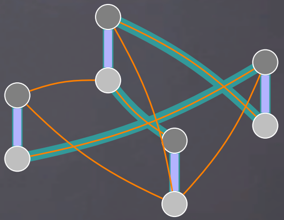
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Lemma

D admits a directed Hamiltonian path $\Leftrightarrow$ M can be covered with a single alternating path in G.

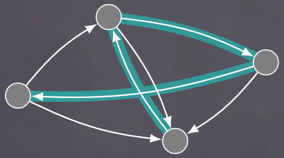
"$\Leftarrow$": contract each matching edge in the covering alternating path.

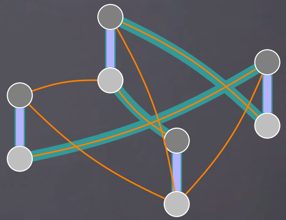
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Lemma

D admits a directed Hamiltonian path $\Leftrightarrow$ M can be covered with a single alternating path in G.

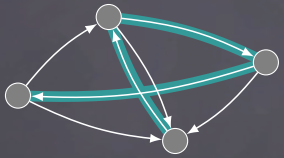
"$\Leftarrow$": contract each matching edge in the covering alternating path.
hits all vertices exactly once ✓ is valid directed path ✓

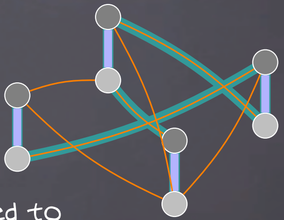
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Theorem

Scaffolding is NP-hard, even restricted to

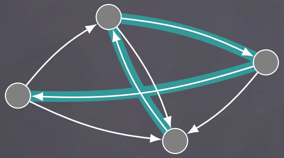
- bipartite graphs
- $(\sigma_p, \sigma_c) \in \{(0,1),(1,0)\}$ and
- $\omega : E \to \{0\}$.

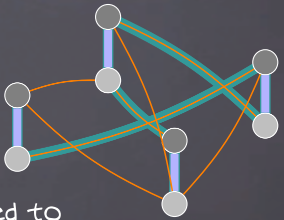
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Theorem

Scaffolding is NP-hard, even restricted to

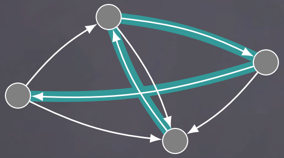
- supergraphs of bipartite graphs
- $(\sigma_p, \sigma_c) \in \{(0,1),(1,0)\}$ and
- $\omega : E \to \{0, 1\}$.

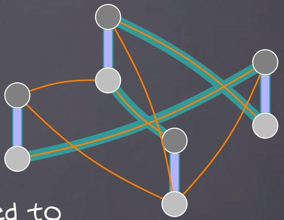
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Theorem

Scaffolding is NP-hard, even restricted to

- supergraphs of bipartite graphs
- $(\sigma_p, \sigma_c) \in \{(0, 1), (1, 0)\}$ and
- $\omega : E \to \{0, 1\}$.

Corollary

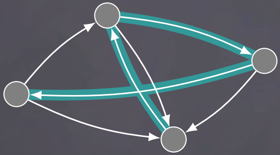
Scaffolding with 2 weights is NP-hard in any sufficiently dense graph class.

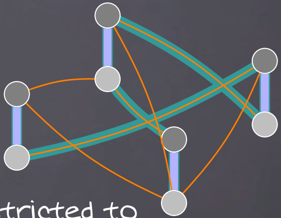
Hardness Warm up: Hamiltonian Path

Recall: Scaffolding

Input: Graph G, perfect matching $\mathcal{M}$, weights ω, $k, \sigma_p, \sigma_c \in \mathbb{N}$

Question: Can G be covered by $\leq \sigma_p$ alternating paths & $\leq \sigma_c$ alternating cycles of total weight $\geq k$?





Theorem

Exact Scaffolding is NP-hard, even restricted to

- supergraphs of bipartite graphs
- $(\sigma_p, \sigma_c) \in \{(0,1),(1,0)\}$ and
- $\omega : E \to \{0, 1\}$.

Corollary

Exact Scaffolding with 2 weights is NP-hard in any sufficiently dense graph class.

Scaffolding in Co-Bipartites

Wait, what?

Scaffolding in Co-Bipartites

Wait, what?

Recap: Corollary

Scaffolding with 2 weights is NP-hard in any sufficiently dense graph class.

Scaffolding in Co-Bipartites

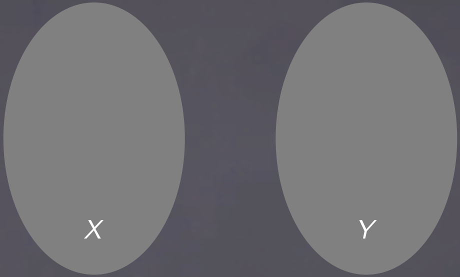
Wait, what?

Recap: Corollary

Scaffolding with 2 weights is NP-hard in any sufficiently dense graph class.

⇝ Unweighted!

Scaffolding in Unweighted Co-Bipartites



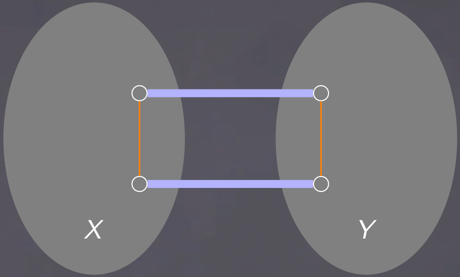
Observation

no edges between X & Y $\rightsquigarrow$ need 2 objects (paths/cycles)
otherwise $\rightsquigarrow$ can always cover G with 1 path

TODO

decide if we can cover with 1 cycle

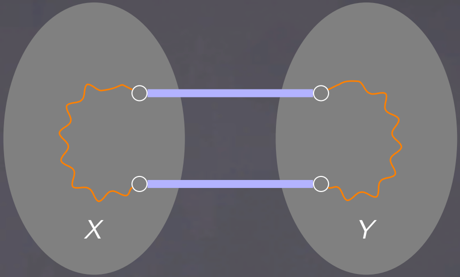
Scaffolding in Unweighted Co-Bipartites



Observation

$\exists$ alternating cycle with non-matching edge X
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

Scaffolding in Unweighted Co-Bipartites



Observation

$\exists$ alternating cycle with non-matching edge X
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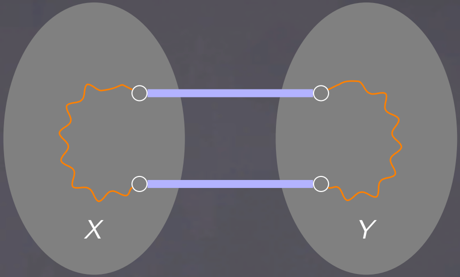
Scaffolding in Unweighted Co-Bipartites



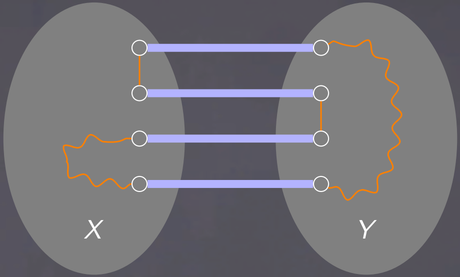
Observation

$\exists$ alternating cycle with non-matching edge X
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

Observation

#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓

Scaffolding in Unweighted Co-Bipartites



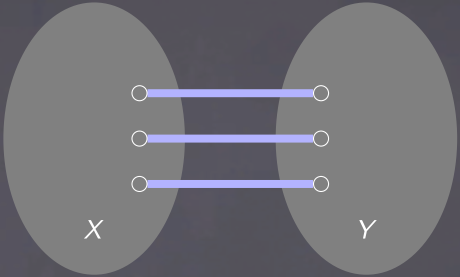
Observation

$\exists$ alternating cycle with non-matching edge X
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

Observation

#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓

Scaffolding in Unweighted Co-Bipartites



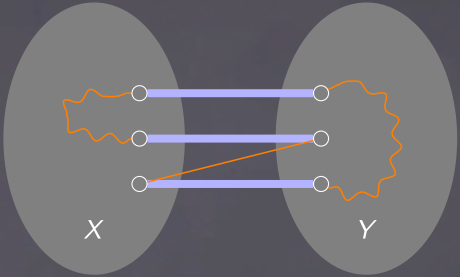
Observation

$\exists$ alternating cycle with non-matching edge X
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

Observation

#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓
#matching edges between X & Y odd

Scaffolding in Unweighted Co-Bipartites



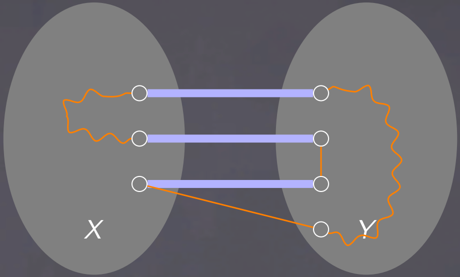
Observation

$\exists$ alternating cycle with non-matching edge X
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

Observation

#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓
#matching edges between X & Y odd
$\rightsquigarrow$ find any non-matching edge between X & Y

Scaffolding in Unweighted Co-Bipartites



Observation

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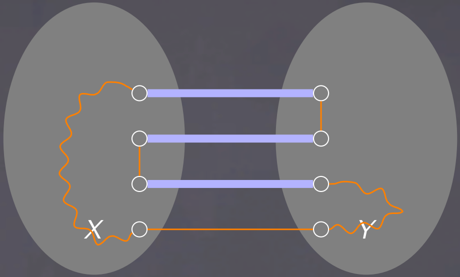
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

Observation

#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓
#matching edges between X & Y odd
$\rightsquigarrow$ find any non-matching edge between X & Y

Scaffolding in Unweighted Co-Bipartites



Observation

$\exists$ alternating cycle with non-matching edge X
$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

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#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓
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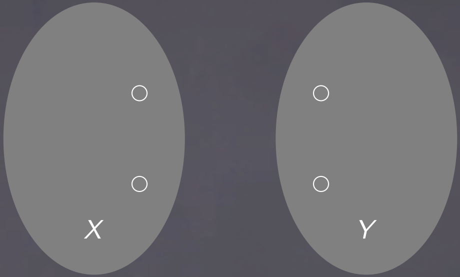

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#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓
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$\rightsquigarrow$ find any non-matching edge between X & Y
#matching edges between X & Y is 0

Scaffolding in Unweighted Co-Bipartites

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$\rightsquigarrow$ extend to cover all $\mathcal{M}$ in $G[X]$

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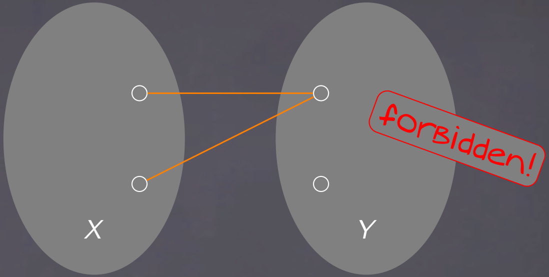
Scaffolding in Unweighted Co-Bipartites



Observation

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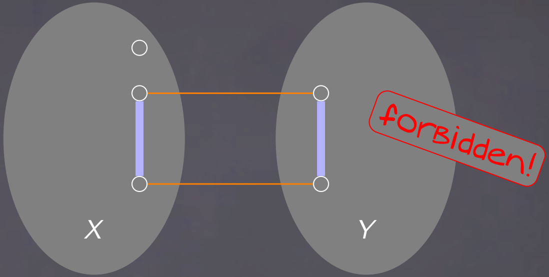

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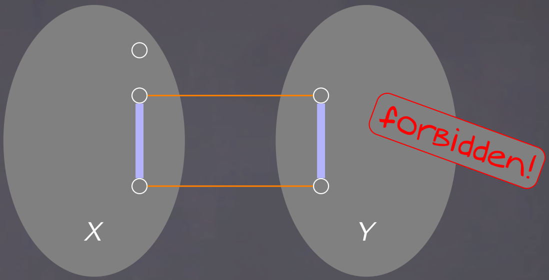
Scaffolding in Unweighted Co-Bipartites



Observation

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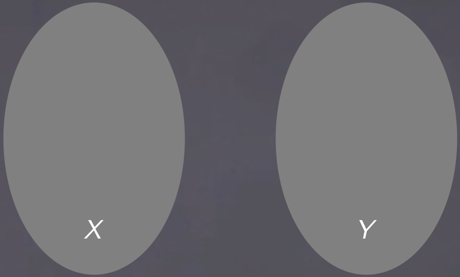
Observation

#matching edges between X & Y even (and > 0) $\rightsquigarrow$ ✓
#matching edges between X & Y odd
$\rightsquigarrow$ find any non-matching edge between X & Y
#matching edges between X & Y is 0
all other cases are ✓ (tedious case analysis)

Scaffolding in Unweighted Co-Bipartites



Theorem

Scaffolding can be solved in $O(n+m)$ time on co-bipartite graphs

Scaffolding in Unweighted Trees

Observation

no alternating cycles in a tree

Scaffolding in Unweighted Trees

Observation

no alternating cycles in a tree

Observation

consider a lowest leaf ℓ

Scaffolding in Unweighted Trees

Observation

no alternating cycles in a tree

Observation

consider a lowest leaf ℓ
$\mathcal{M}$ is perfect $\rightsquigarrow$ ℓ matched

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Scaffolding in Unweighted Trees

Observation

no alternating cycles in a tree

Observation

consider a lowest leaf ℓ
$\mathcal{M}$ is perfect $\rightsquigarrow$ ℓ matched
parent p of ℓ has only 1 child

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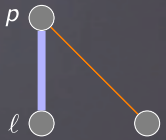

Scaffolding in Unweighted Trees

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Scaffolding in Unweighted Trees

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Observation

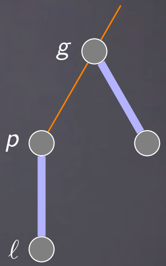
consider a lowest leaf ℓ

$\mathcal{M}$ is perfect $\rightsquigarrow$ ℓ matched

parent p of ℓ has only 1 child

Case 1

parent g of p is matched "below"



Scaffolding in Unweighted Trees

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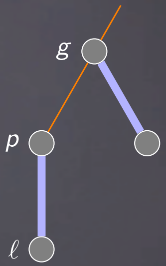

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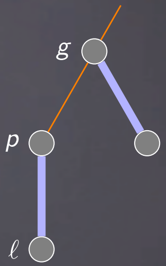
$\rightsquigarrow$ always take $\ell - p - g - \ell'$



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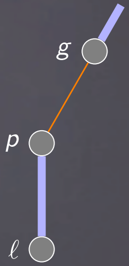

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$\leadsto$ g is matched to a leaf ℓ'
$\leadsto$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"

Scaffolding in Unweighted Trees

Observation

no alternating cycles in a tree

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$\mathcal{M}$ is perfect $\leadsto$ ℓ matched

parent p of ℓ has only 1 child

Case 1

parent g of p is matched "below"

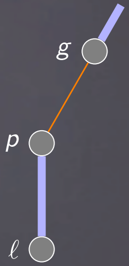
$\leadsto$ g is matched to a leaf ℓ'

$\leadsto$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"

either p is the only child of g



Scaffolding in Unweighted Trees

Observation

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Observation

consider a lowest leaf ℓ
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parent p of ℓ has only 1 child

Case 1

parent g of p is matched "below"
$\rightsquigarrow$ g is matched to a leaf ℓ'
$\rightsquigarrow$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"
either p is the only child of g $\rightsquigarrow$ delete ℓ & g and reduce k

Scaffolding in Unweighted Trees

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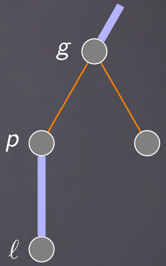
no alternating cycles in a tree

Observation

consider a lowest leaf ℓ

$\mathcal{M}$ is perfect $\rightsquigarrow$ ℓ matched

parent p of ℓ has only 1 child



Case 1

parent g of p is matched "below"

$\rightsquigarrow$ g is matched to a leaf ℓ'

$\rightsquigarrow$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"

either p is the only child of g $\rightsquigarrow$ delete ℓ & g and reduce k

or g has another child u

Scaffolding in Unweighted Trees

Observation

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Observation

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$\mathcal{M}$ is perfect $\leadsto$ ℓ matched
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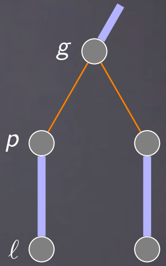

Case 1

parent g of p is matched "below"
$\leadsto$ g is matched to a leaf ℓ'
$\leadsto$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"
either p is the only child of g $\leadsto$ delete ℓ & g and reduce k
or g has another child u $\leadsto$ u matched "below"

Scaffolding in Unweighted Trees

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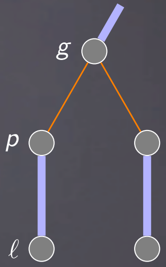

Case 1

parent g of p is matched "below"
$\rightsquigarrow$ g is matched to a leaf ℓ'
$\rightsquigarrow$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"
either p is the only child of g $\rightsquigarrow$ delete ℓ & g and reduce k
or g has another child u $\rightsquigarrow$ u matched "below" $\rightsquigarrow$ $\exists$ "clone" of $g - p - \ell$

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Observation

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Observation

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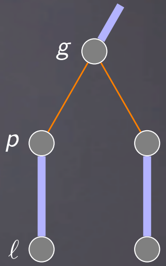

Case 1

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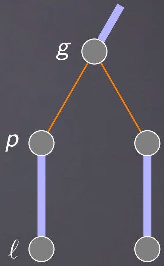
$\rightsquigarrow$ always take $\ell - p - g - \ell'$

Case 2

parent g of p is matched "above"
either p is the only child of g $\rightsquigarrow$ delete ℓ & g and reduce k
or g has another child u $\rightsquigarrow$ u matched "below" $\rightsquigarrow$ $\exists$ "clone" of $g - p - \ell$
$\rightsquigarrow$ take $p - \ell$

Scaffolding in Unweighted Trees



Theorem

Scaffolding can be solved in $O(n)$ time on unweighted trees

Scaffolding in Weighted Trees

Dynamic Programming Idea

Bottom-up traversal; in each vertex v, need to remember:

- #paths used below v
- v incident with non-matching?

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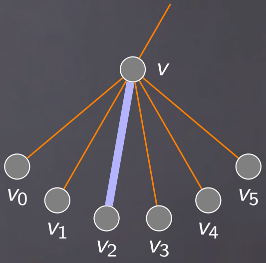
Semantics

$[p, x]_v$ = max. weight collected below v with p finished paths "under x"



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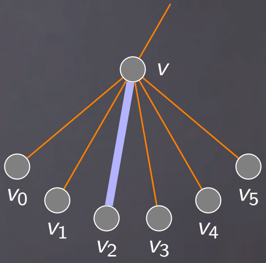

Recurrence

Let $v_1, v_2, \ldots, v_c$ be the children of v.

$$[p, \text{✗}]_v := \max_{\substack{p_1, p_2, \ldots, p_c \\ \sum p_i = p}} \sum_{1 \le i \le c} \max_{x \in \{\text{✓}, \text{✗}\}} [p_i, x]_{v_i}$$

Scaffolding in Weighted Trees

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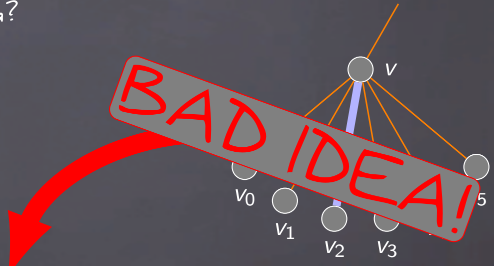


Recurrence

Let $v_1, v_2, \ldots, v_c$ be the children of v.

$$[p, \times]_v := \max_{\substack{p_1, p_2, \ldots, p_c \\ \sum p_i = p}} \sum_{1 \le i \le c} \max_{x \in \{\checkmark, \times\}} [p_i, x]_{v_i}$$

Scaffolding in Weighted Trees

Dynamic Programming Idea

Bottom-up traversal; in each vertex v, need to remember:

- #paths used below v
- v incident with non-matching?

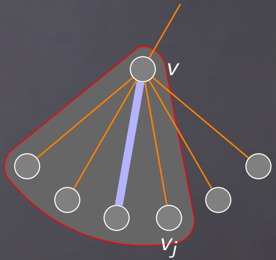
Semantics

$[j, p, x]_v$ = max. weight collected below v with p finished paths "under x" up to v_j

(abbrev: last child $\rightsquigarrow [p, x]_v$)

Recurrence

Let $v_1, v_2, \ldots, v_c$ be the children of v.



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Bottom-up traversal; in each vertex v, need to remember:

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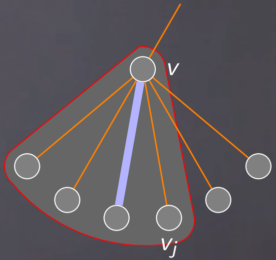

Recurrence

Let $v_1, v_2, \ldots, v_c$ be the children of v.

$[0, 0, \cancel{x}]_v := 0$

$$[j, p, x]_v := \max_{p_j \leq p} \left\{ \right.$$

Scaffolding in Weighted Trees

Dynamic Programming Idea

Bottom-up traversal; in each vertex v, need to remember:

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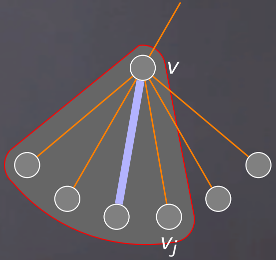

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Let $v_1, v_2, \ldots, v_c$ be the children of v.

$$[0, 0, \times]_v := 0$$

$$[j, p, x]_v := \max_{p_j \leq p} \begin{cases} \max\{[p_j, \checkmark]_{v_j}, [p_j, \times]_{v_j}\} + [j-1, p-p_j, x]_v & \text{if } vv_j \notin \mathcal{M} \end{cases}$$

Scaffolding in Weighted Trees

Dynamic Programming Idea

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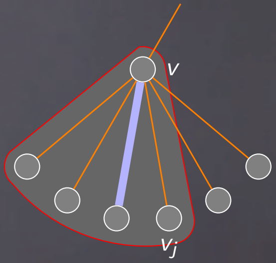

Semantics

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Recurrence

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Scaffolding in Weighted Trees

Dynamic Programming Idea

bottom-up traversal; in each vertex v, need to remember:

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Semantics

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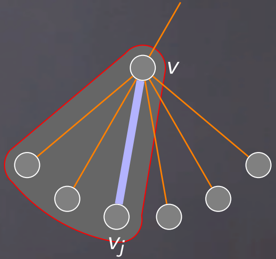

Recurrence

Let $v_1, v_2, \ldots, v_c$ be the children of v.

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Scaffolding in Weighted Trees

Dynamic Programming Idea

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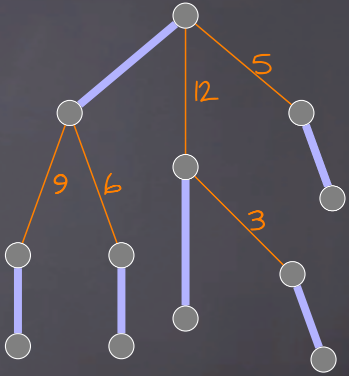

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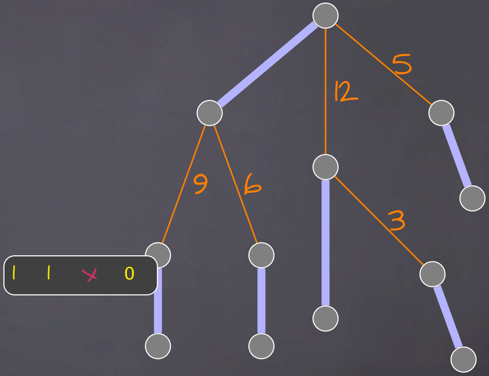

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Scaffolding in Weighted Trees

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Bottom-up traversal; in each vertex v, need to remember:

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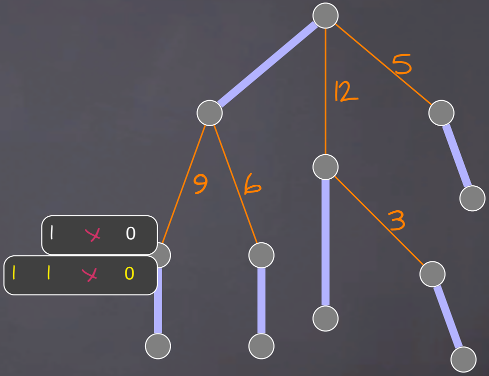

Recurrence

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Scaffolding in Weighted Trees

Dynamic Programming Idea

Bottom-up traversal; in each vertex v, need to remember:

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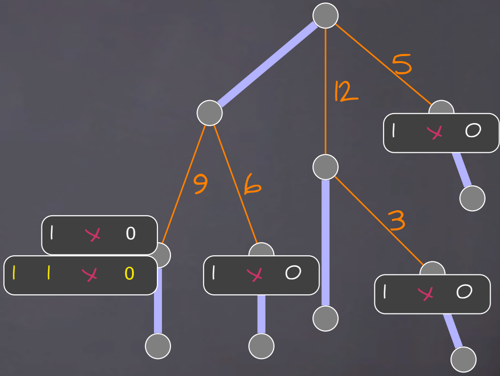

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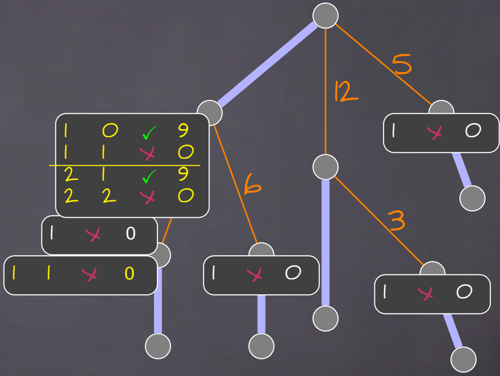

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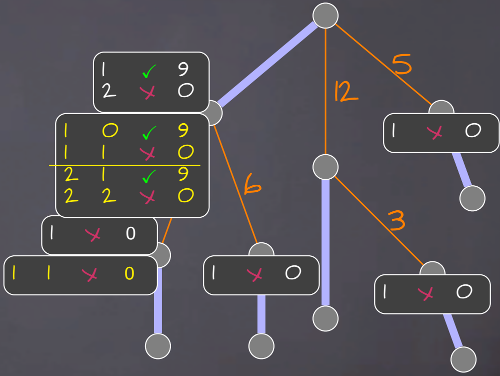

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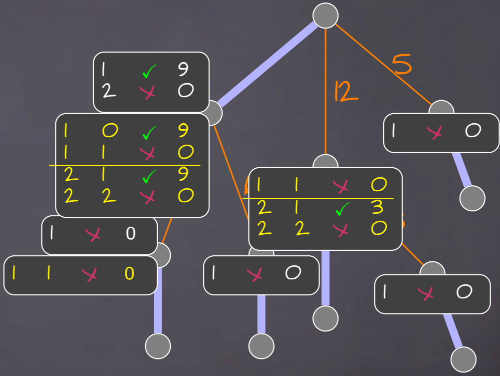

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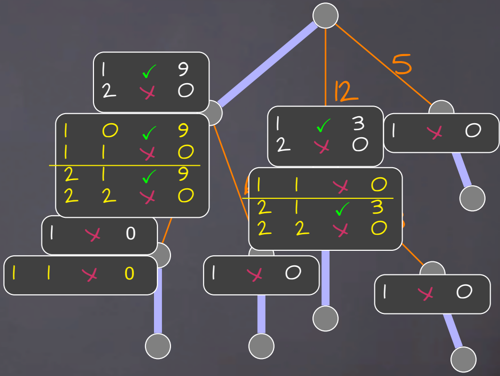

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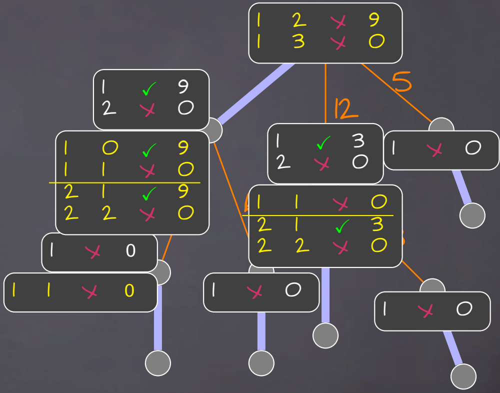

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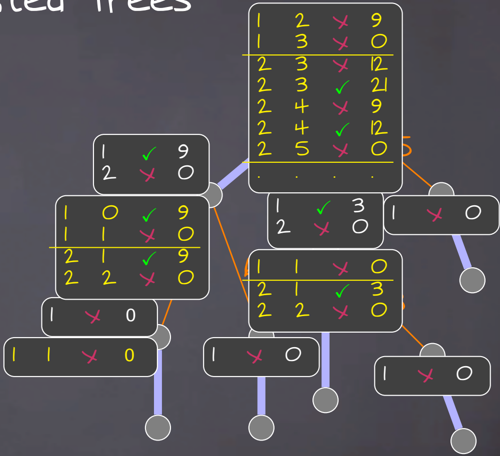
Scaffolding in Weighted Trees



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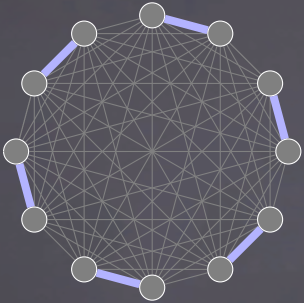
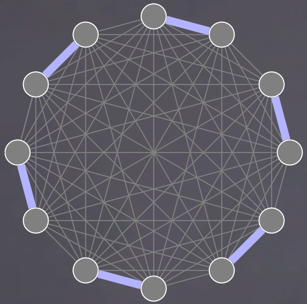


$\sigma_p = 1$, $\sigma_c = 1$?

Approximate Scaffolding

3-Approximation in Dense Graphs



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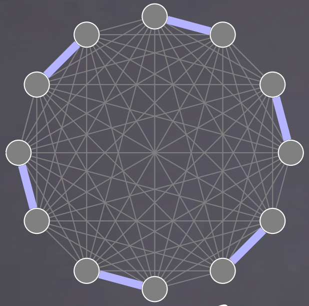

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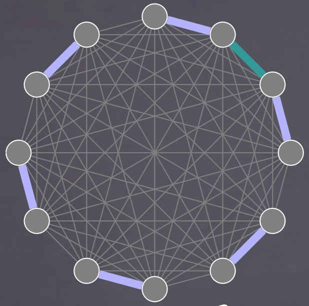
2. repeatedly take heaviest edge, if possible

3-Approximation in Dense Graphs



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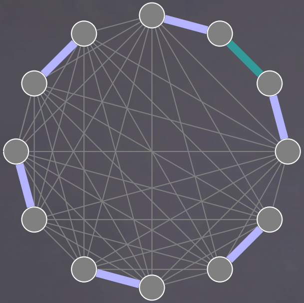

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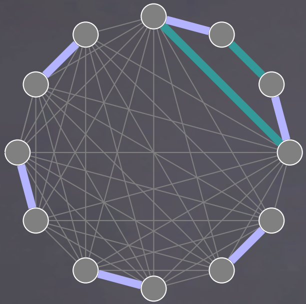

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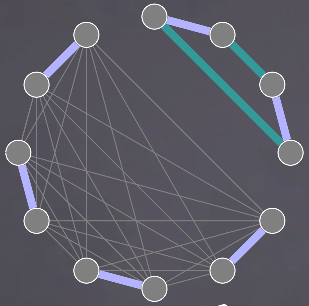

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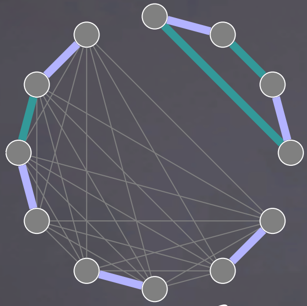

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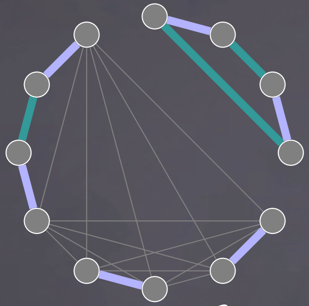

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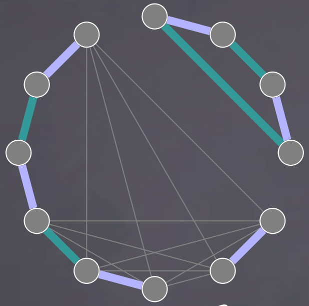

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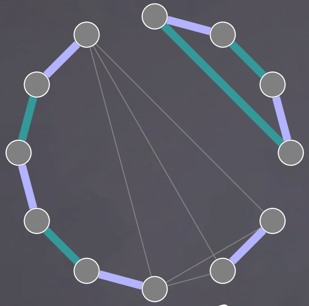

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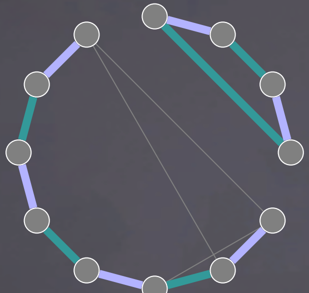

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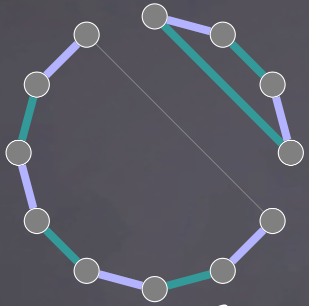

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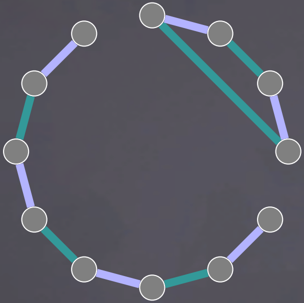

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Approximate Scaffolding

1. sort all edges by weight
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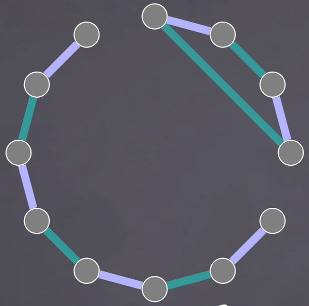
Proof

Result S^* is a valid solution ✓

3-Approximation in Dense Graphs



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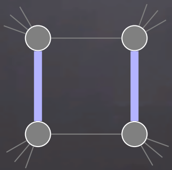
Result S^* is a valid solution ✓
Note: taking an edge forbids ≤ 3 OPT edges



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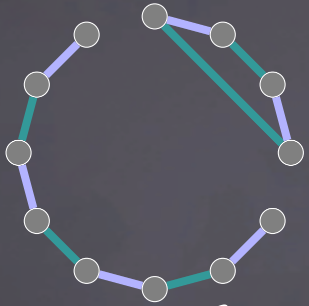

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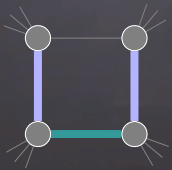

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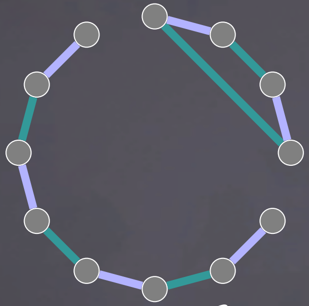

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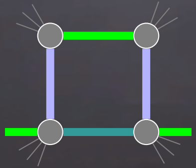

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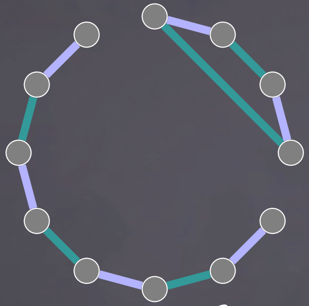

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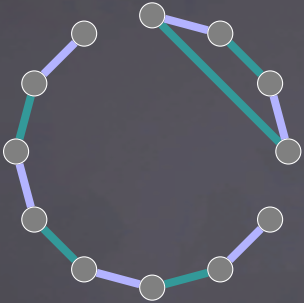
Note: taking an edge forbids ≤ 3 OPT edges

$\rightsquigarrow$ mark the ≤ 3 OPT-edges when taking an edge e

$\rightsquigarrow$ e is heaviest among them

$\rightsquigarrow$ $3\omega(S^*) \geq OPT$

3-Approximation in Dense Graphs



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Approximate Scaffolding

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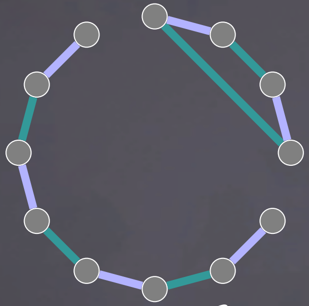
Theorem

Scaffolding in complete graphs can be 3-approximated in $O(|V| \log |V|)$ time.

3-Approximation in Dense Graphs



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Theorem

Scaffolding in complete (bipartite) graphs can be 3-approximated in $O(|V| \log |V|)$ time.

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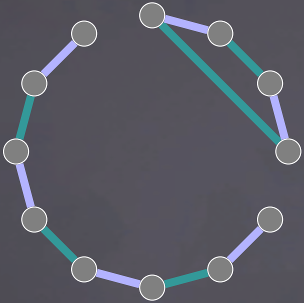

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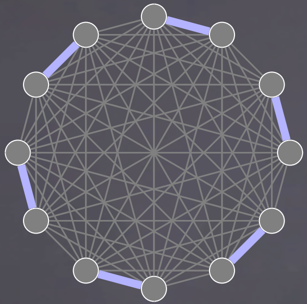
Scaffolding in complete (bipartite) graphs can be 3-approximated in $O(|V| \log |V|)$ time.

Remark

For Exact Scaffolding, we have to keep an eye on the number of components too.

2-Approximation in Dense Graphs



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Approximate Exact Scaffolding

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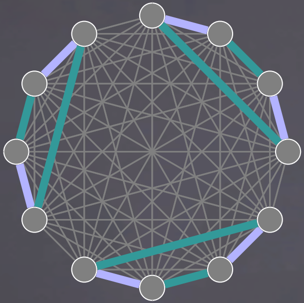
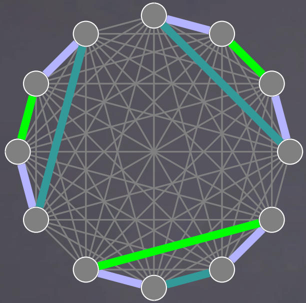


$\sigma_p = 1, \sigma_c = 1?$

Approximate Exact Scaffolding

1. compute max.-weight perfect matching S
   $\rightsquigarrow$ $S \cup \mathcal{M}$ is collection of cycles

2-Approximation in Dense Graphs



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Approximate Exact Scaffolding

1. compute max.-weight perfect matching S
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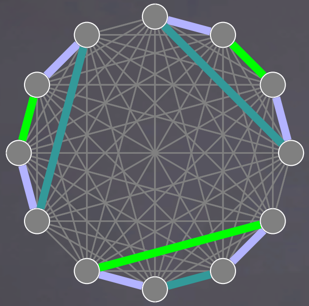

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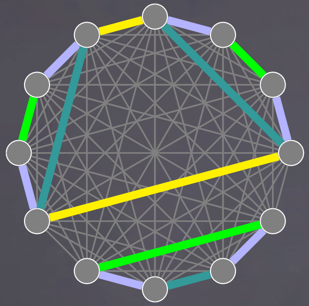

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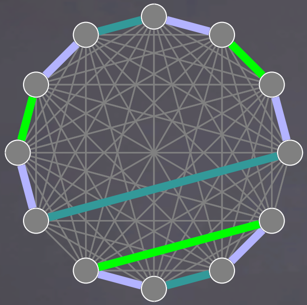

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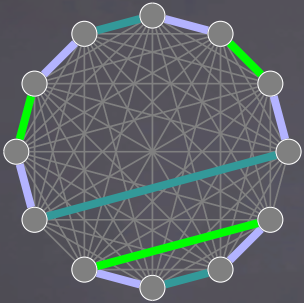

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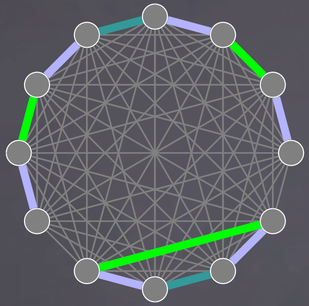

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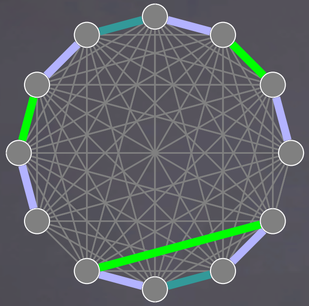

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Proof

Result S^* is a valid solution ✓

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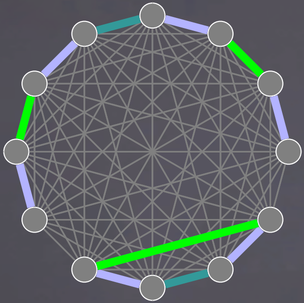

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$\omega(S^*) \geq \omega(\mathit{fix}) \geq {}^{\omega(S)}/_2 \geq {}^{OPT}/_2$

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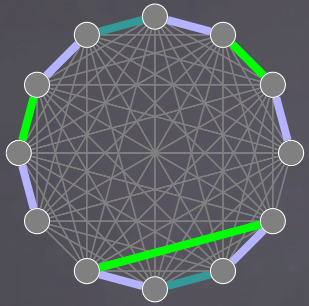

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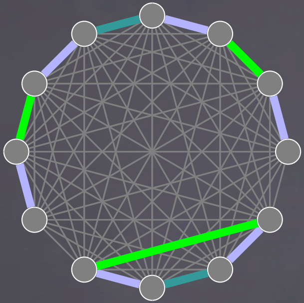
Theorem

Exact Scaffolding in complete graphs can be 2-approximated in $O(|V|^2)$ time.

2-Approximation in Dense Graphs



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Exact Scaffolding in complete (bipartite) graphs can be 2-approximated in $O(|V|^2)$ time.

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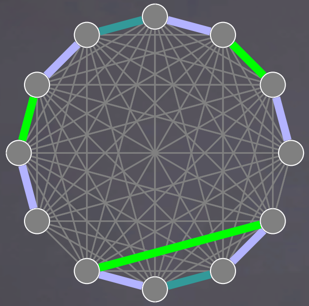

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Remark

For Scaffolding, replace Step 3 by either merging cycles or removing lightest edge, whatever looses less weight

Exact Algorithms I: Brute Force

Observation

An ordering of $V(G)$ certifies YES-instances of Scaffolding.

Exact Algorithms I: Brute Force

$[p, c, j]_i :=$ max. weight collectible before v_i with p & c paths/cycles plus one path starting at v_j

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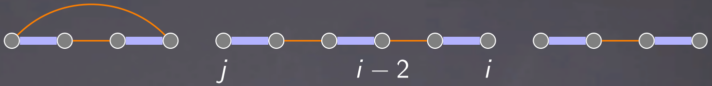

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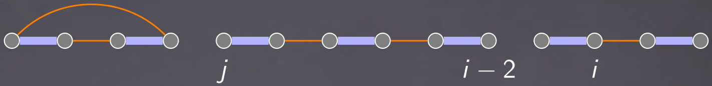

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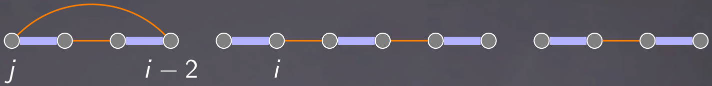

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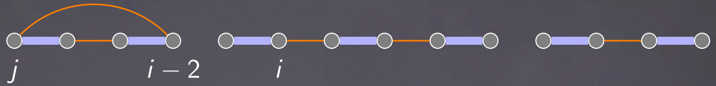

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An ordering of $V(G)$ certifies YES-instances of Scaffolding.

$\rightsquigarrow$ try all $O(n!)$ certificates

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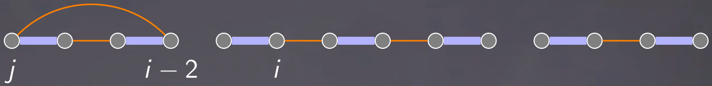

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Exact Algorithms II: Dynamic Programming

Semantics

$[S, p, c, u, v]$ = max. weight collectible in $G[S]$ by p alt. paths, c alt. cycles and an alt. path starting at u & ending at v

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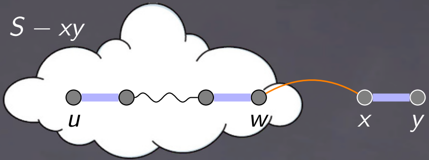

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Let $xy \in \mathcal{M}$. Then, $[\{xy\}, 0, 0, x, y] := 0$ and

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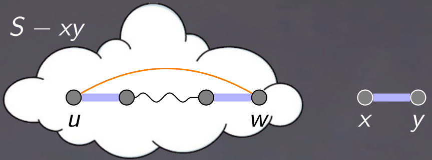

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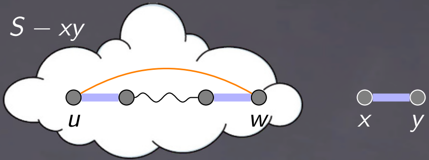

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Theorem

Scaffolding can be solved in $O(\sqrt{2}^n n^3 \sigma_p \sigma_c)$ time.

Sparse Graphs: Quasi-Forest

Recall

- Scaffolding is hard in any sufficiently dense graph class
- Scaffolding is easy in trees

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A Shot at Sparsity

G is Quasi-forest $\Leftrightarrow$ $G - \mathcal{M}$ is forest

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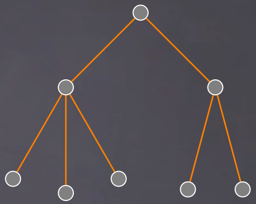

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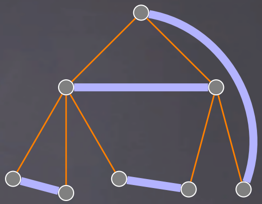

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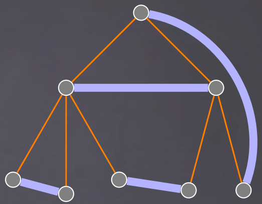

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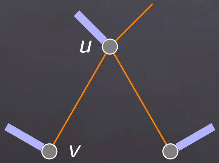

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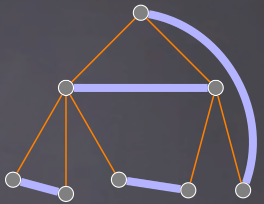

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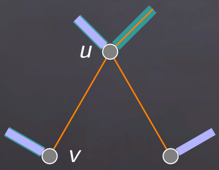

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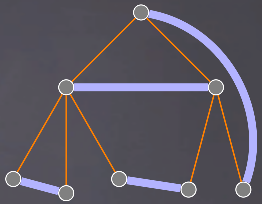

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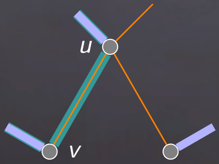

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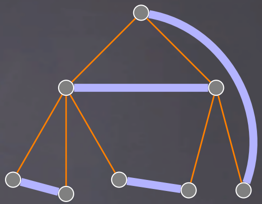

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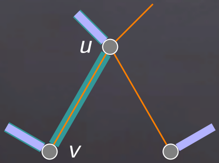

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  unless it's the same path!

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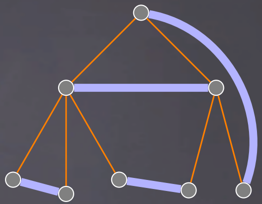

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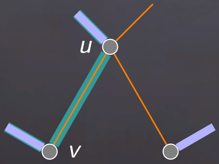

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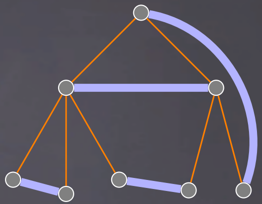
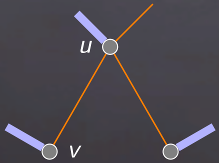
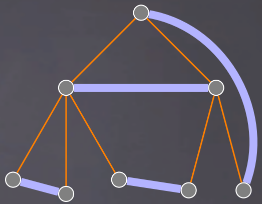


Observation

Each leaf v of $G - \mathcal{M}$ has degree 2 in G
$\rightsquigarrow$ if $\sigma_p = 0$, we have to take both!



Sparse Graphs: Quasi-Forest



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- Scaffolding is hard in any sufficiently dense graph class
- Scaffolding is easy in trees

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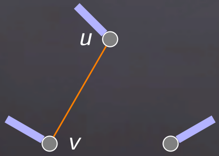

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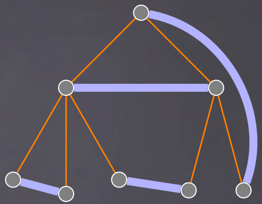

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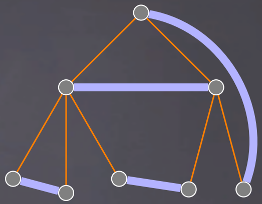

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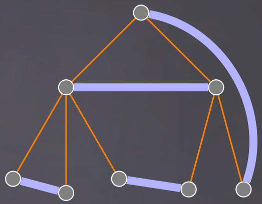

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But is it even NP-hard?

Sparse Graphs: Quasi-Forest

Weighted 2-SAT

Input: φ on X in 2-CNF, weights $\omega : X \times \{0,1\} \to \mathbb{N}$, $k \in \mathbb{N}$

Question: is there a satisfying assignment for φ of weight $\leq k$?

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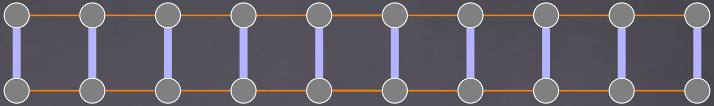
Remark

Independent Set is special case of Weighted 2-SAT

Sparse Graphs: Quasi-Forest



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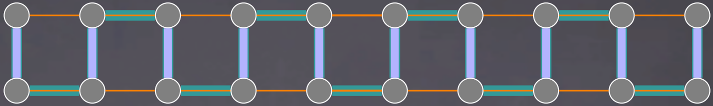

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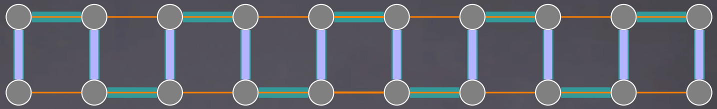

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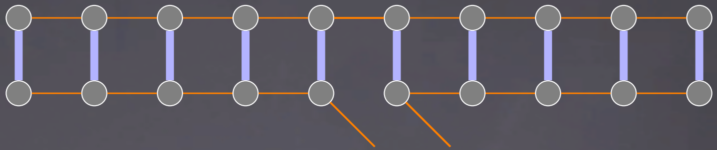

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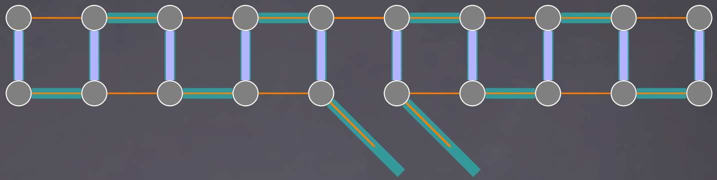

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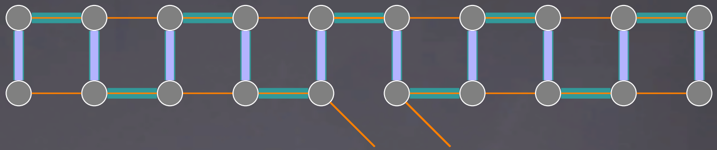

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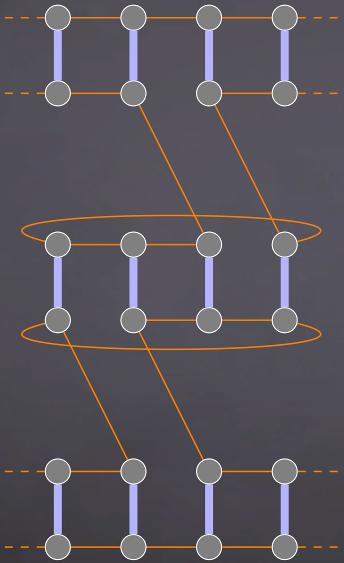

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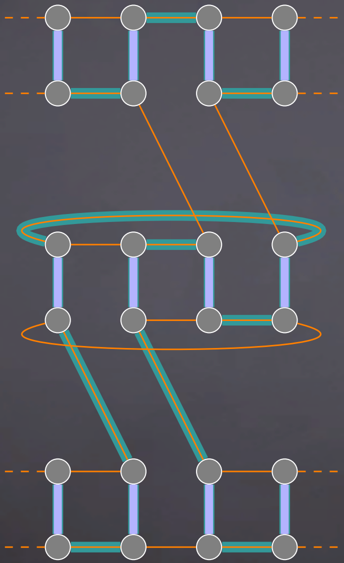

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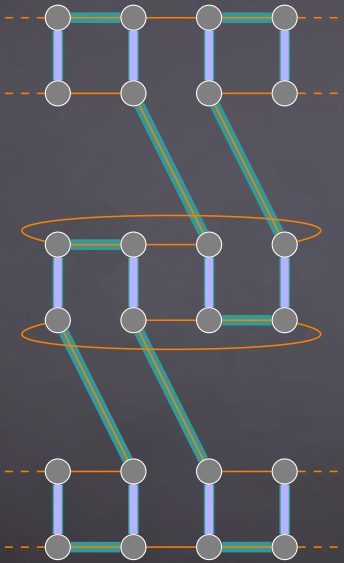

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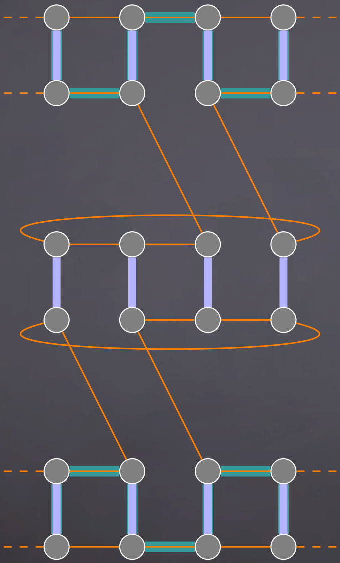

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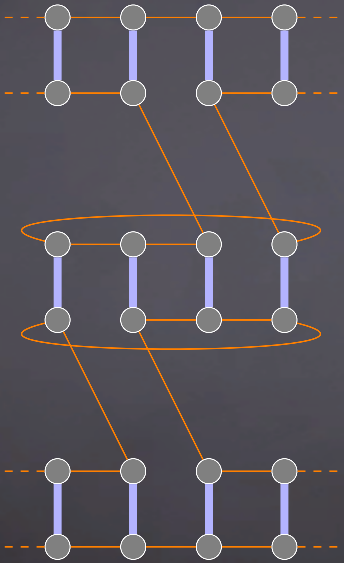

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$\exists$ weight-k satisfying assignment

$\Leftrightarrow$

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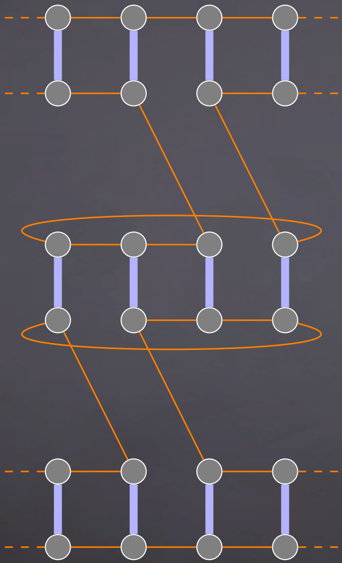

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Scaffolding is NP-hard even if $G - \mathcal{M}$ is a collection of paths with weights 0/1

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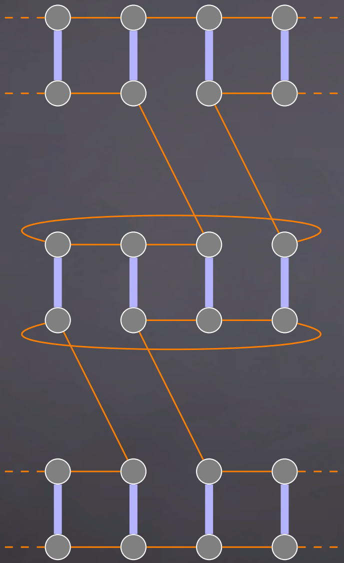

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Corollary

no $2^{o(n+m)}$-time algorithm (ETH)
no $n^{o(k)}$-time algorithm (FPT$\neq$W[t])

Other Forms of Tree-Likeness

Tree Decompositions

tree T, each vertex i associated to some $X_i \subseteq V(G)$ s.t.

1. $\forall\, e \in E(G)$, there is some $i \in V(T)$ with $e \in X_i$
2. $\forall\, v \in V(G)$, bags containing v induce a connected subtree

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Practical instances of Scaffolding have low treewidth (they originate from linear structure)

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Nice Decompositions

Leaf: $X = \varnothing$

Introduce v: i has single child j and $X_i \setminus X_j = \{v\}$

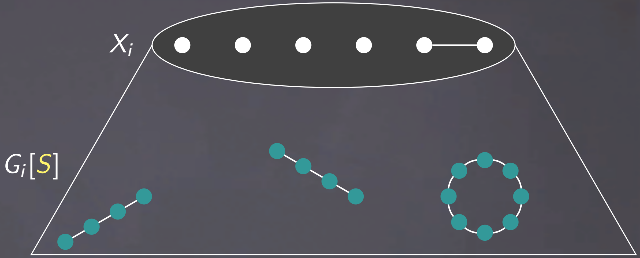
Forget v: i has single child j and $X_j \setminus X_i = \{v\}$

Introduce uv: i has single child j and $uv \subseteq X_i = X_j$

(each edge introduced exactly once)

Join: i has 2 children j and ℓ and $X_i = X_j = X_\ell$

How do Solutions Interact with Bags?



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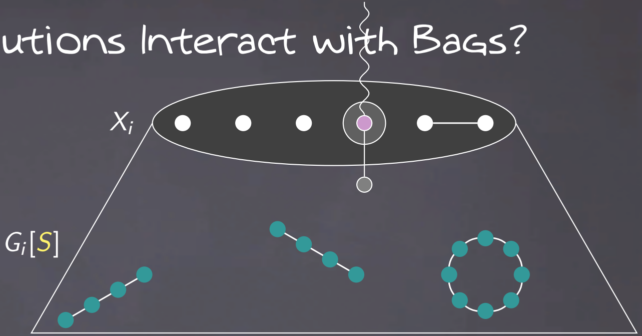

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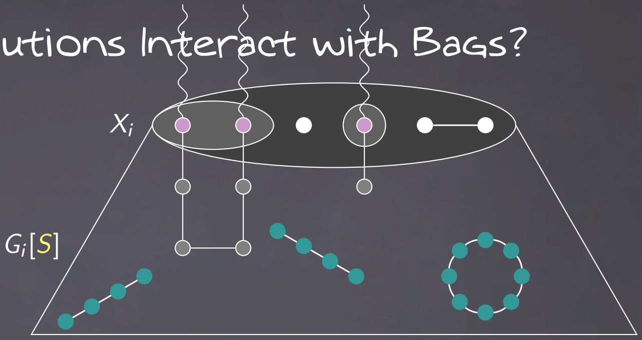

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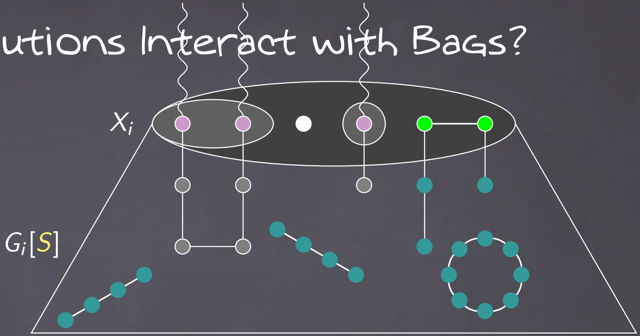

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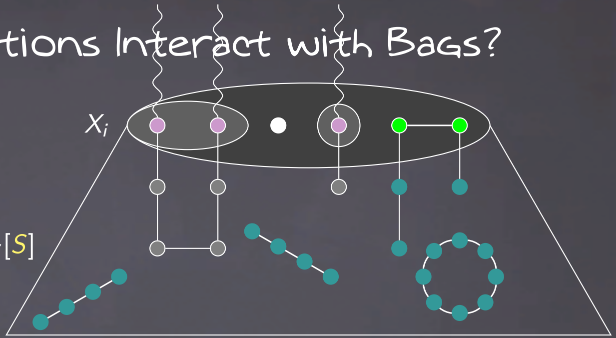

Ingredients

- degree-function $d : X \to \{0, 1, 2\}$
- "pairing" $\subseteq \binom{X}{2} \cup X$
- #paths and #cycles completed "below the bag"

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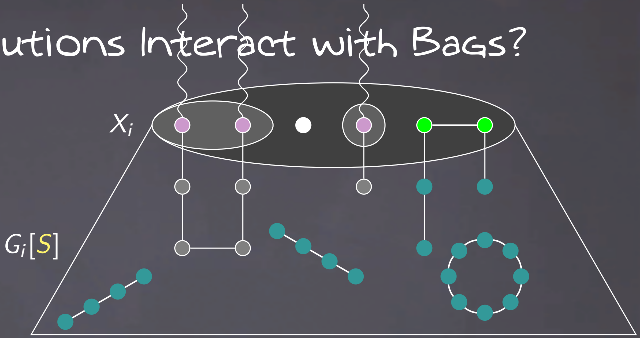

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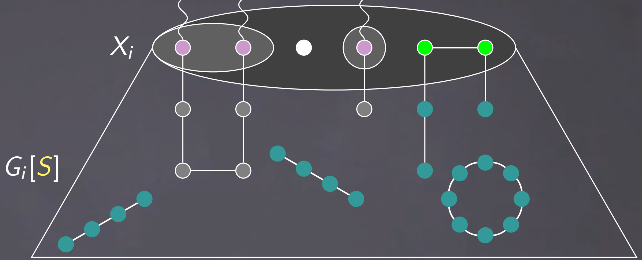

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Semantics

$[d, P, p, c]_i =$ max. weight of any S with $\mathcal{M} \cap E(G_i) \subseteq S \subseteq E(G_i)$ and

1. each vertex $v \in X_i$ has degree $d(v)$ in $G_i[S]$,
2. for each $uv \in P$, $G_i[S]$ contains an alternating path…
   $u = v$: …from u avoiding $d^{-1}(1)$
   $u \neq v$: …from u to v
3. $G_i[S]$ contains p alt. paths & c alt. cycles avoiding $d^{-1}(1)$

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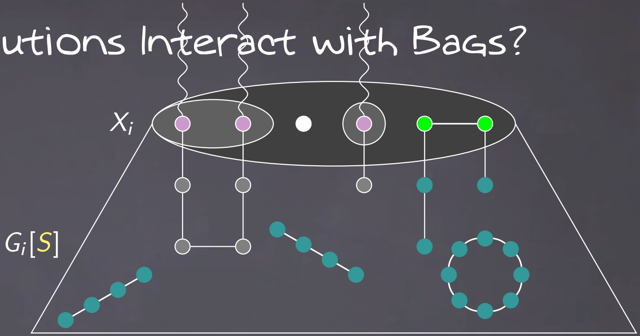

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Leaf Bag

$[\varnothing, \varnothing, 0, 0]_i = 0$

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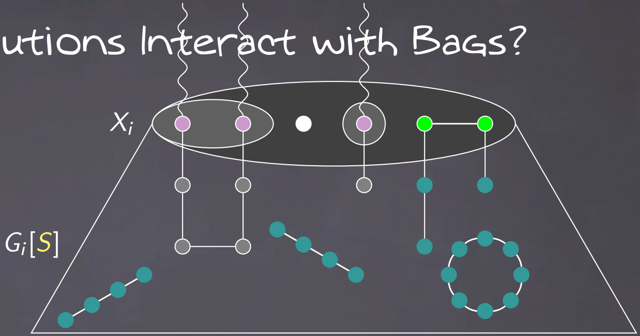

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Introduce v (single child j)

$[d, P, p, c]_i = [d|_{v \to \bot}, P, p, c]_j$

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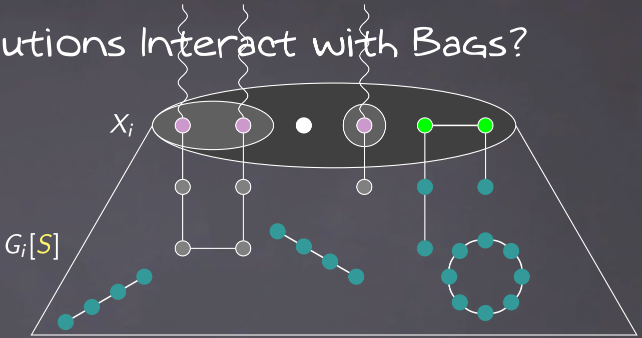

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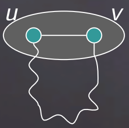
Introduce uv (single child j)

Case 1: $d(u) = d(v) = 2$



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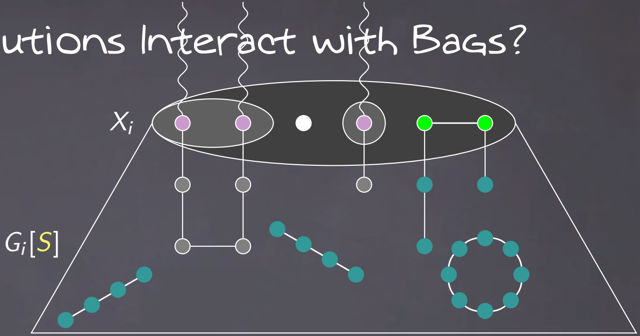

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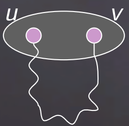

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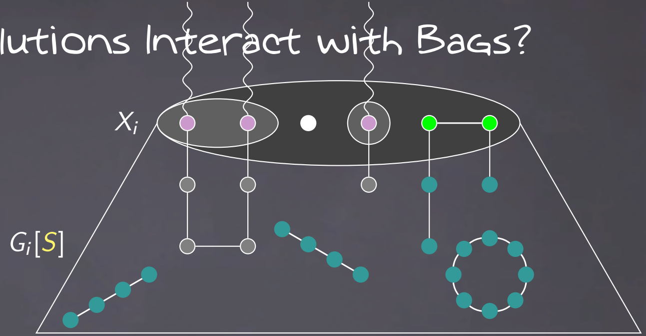

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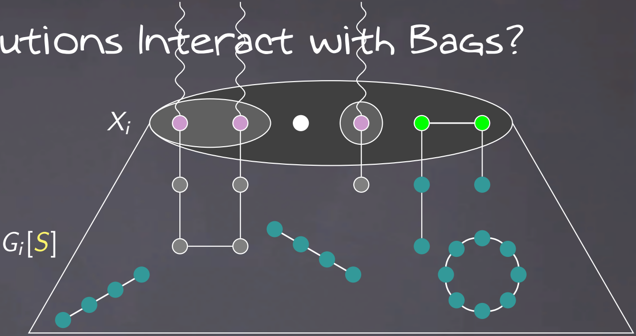

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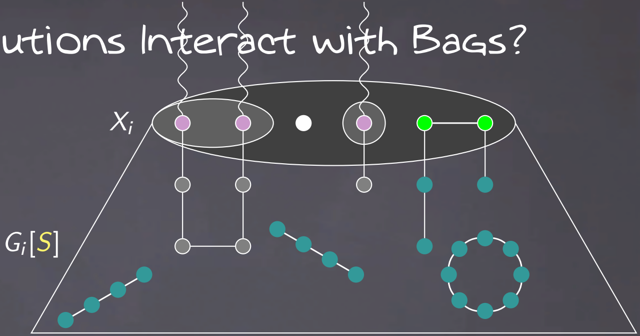

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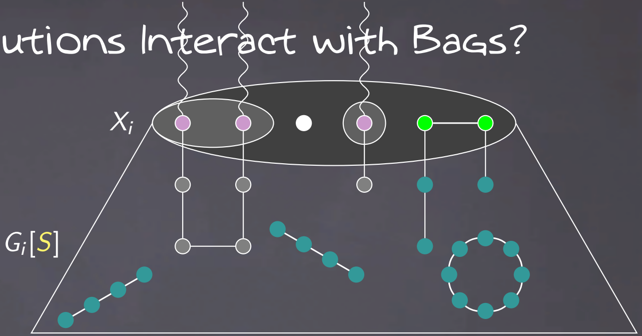

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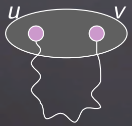

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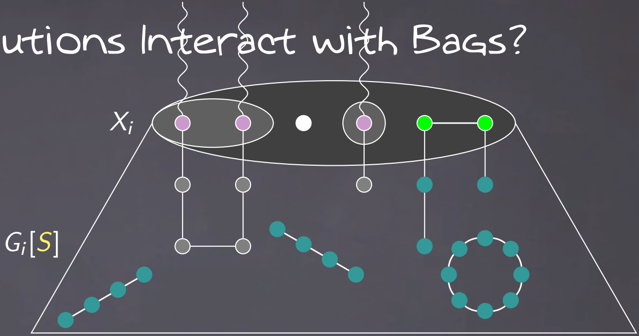

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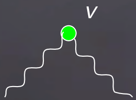

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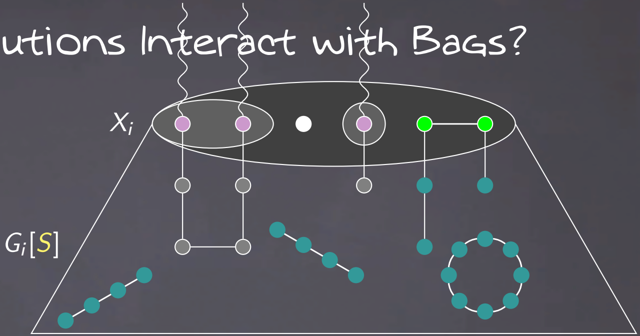

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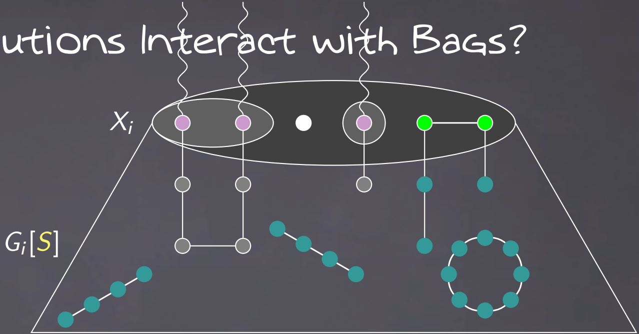
Join Bag (children j & ℓ)

$$[d, P, p, c]_i = \max_{d_j, P_j, p_j, c_j} \max_{\substack{P_\ell \\ P_j \sqcup P_\ell = P}} [d_j, P_j, p_j, c_j]_j + [d - d_j, P_\ell, p - p_j, c - c_j]_\ell$$

How do Solutions Interact with Bags?



Ingredients

- degree-function $d : X \to \{0, 1, 2\}$
- "pairing" $\subseteq \binom{X}{2} \cup X \rightsquigarrow$ #matchings possibilities $\rightsquigarrow O(|X|^{|X|/2})$
- #paths and #cycles completed "below the bag"

Join Bag (children j & ℓ)

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$\rightsquigarrow O(3^{\text{tw}} \cdot \text{tw}^{\text{tw}/2} \cdot \sigma_p \cdot \sigma_c)$ table entries

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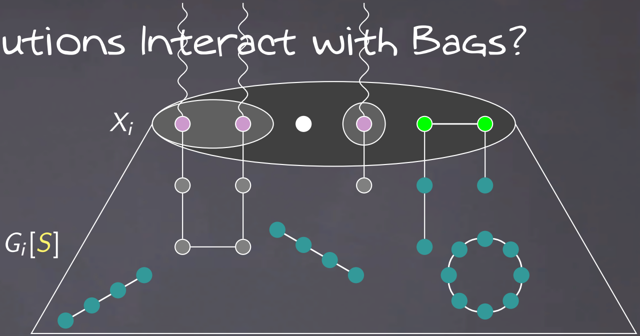

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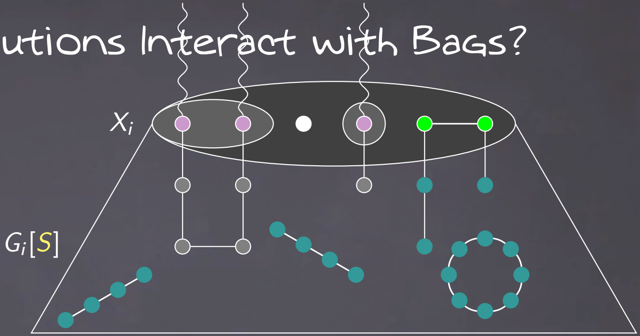
How do Solutions Interact with Bags?



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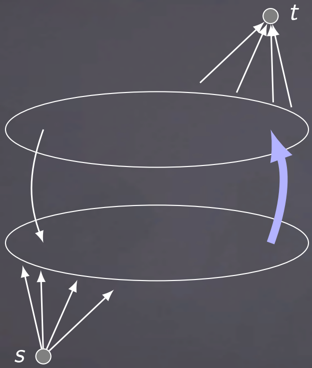
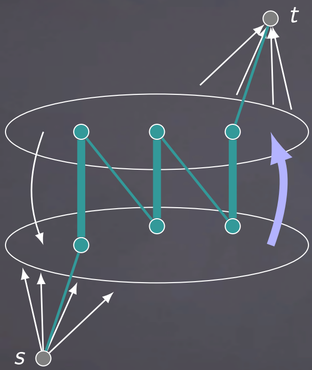
$\rightsquigarrow O(2^{\text{tw}} \cdot \text{tw}^{\text{tw}/2} \cdot \sigma_p \cdot \sigma_c)$ table entries and $O((\text{tw} + 2)^{\text{tw}} \cdot \sigma_p \cdot \sigma_c \cdot n)$ time


Too slow
in prac-
tice!

Integer Linear Program Formulation

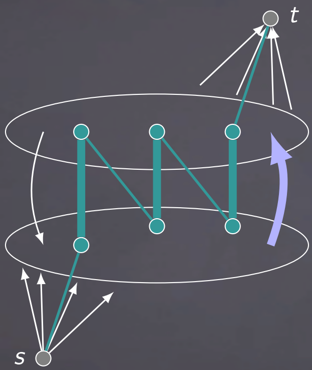


Integer Linear Program Formulation



- chromosomes = disjoint s-t-paths

Integer Linear Program Formulation



- chromosomes = disjoint s-t-paths
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  $x_{\{u,v\}} = y_{uv} + y_{vu}$
- force contigs: $\forall_{uv \in M} x_{uv} = 1$
- path preservation: $\forall_{u \neq s,t} \sum_v y_{vu} = \sum_v y_{uv}$
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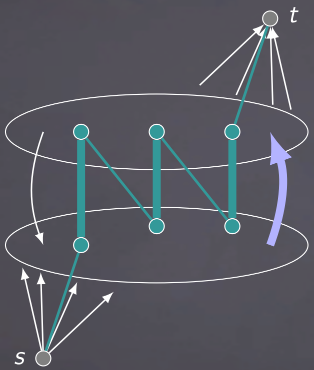
Integer Linear Program Formulation



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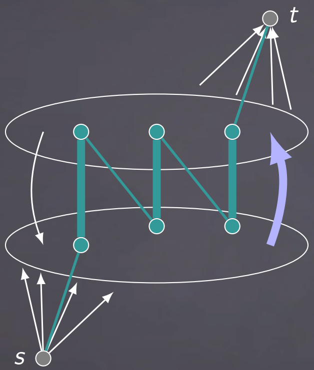

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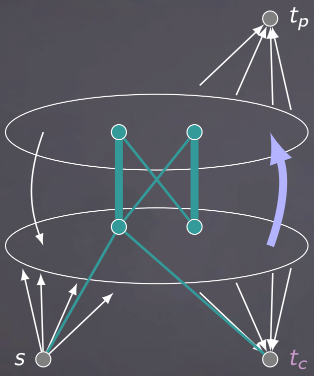

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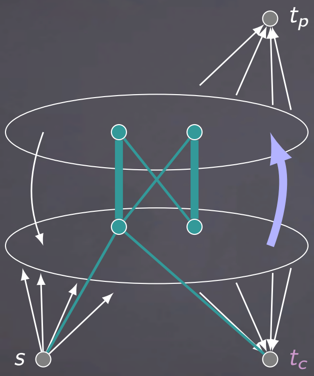

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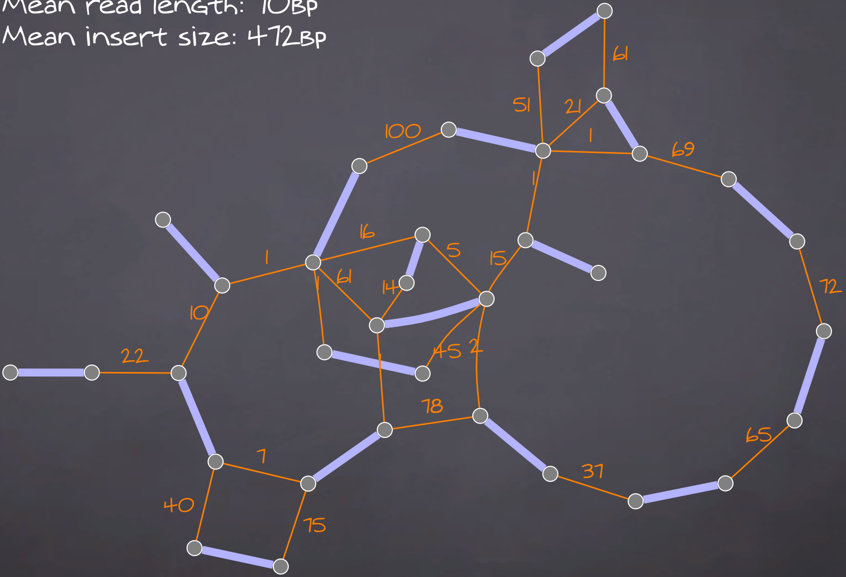
Extension: Contig Jumps

Mean read length: 70bp
Mean insert size: 472bp



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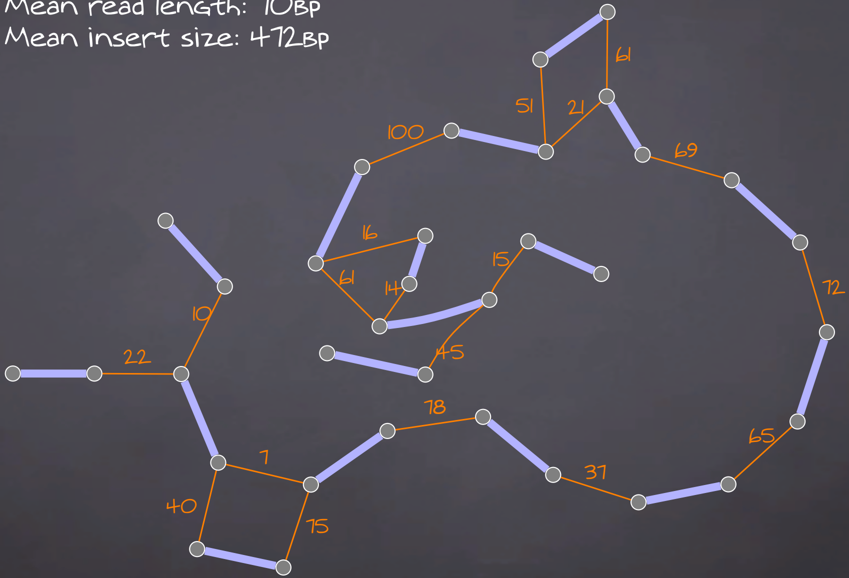

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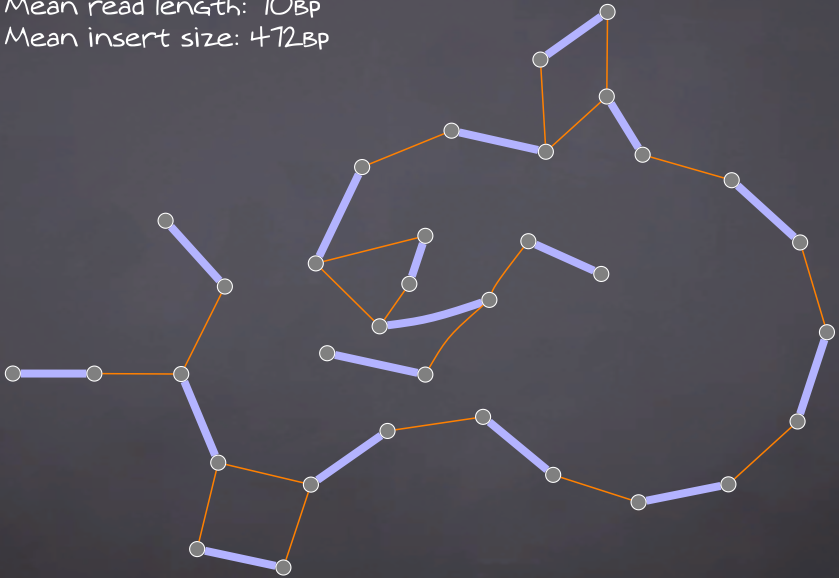

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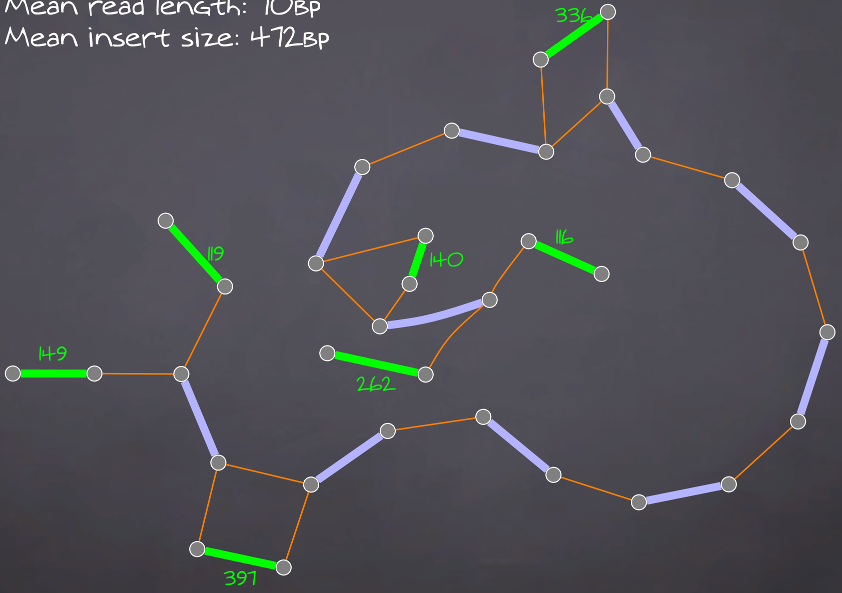

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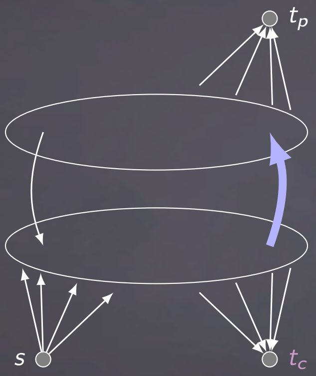

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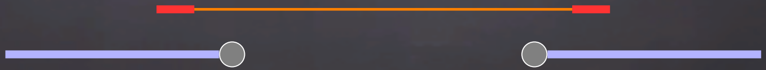

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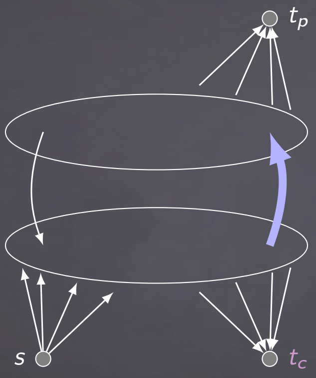

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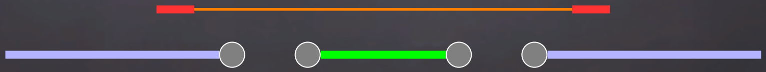

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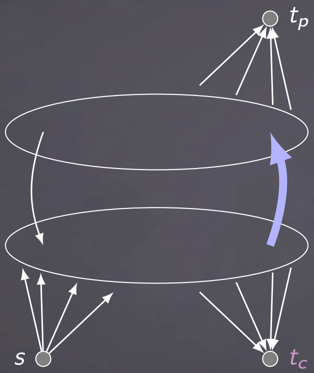

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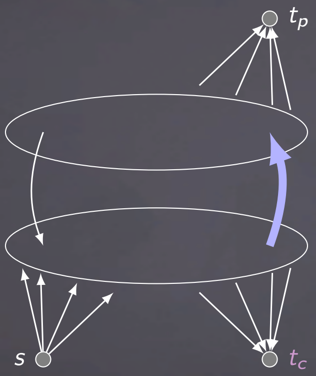

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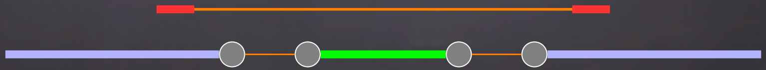

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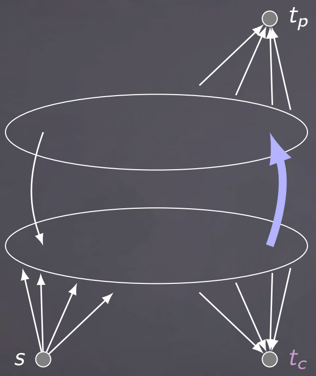

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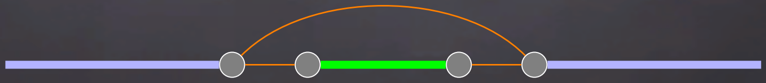

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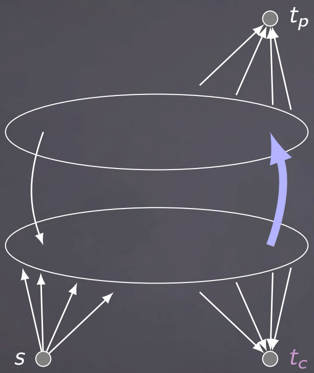

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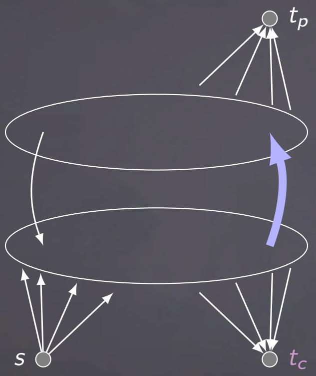
Jump Mechanics

for each non-contig uv,

1. introduce a variable z_{uv}
2. construct "jump network" between u and v that fits in the gap
3. add z_{uv} to $x_{\{u,v\}}$

extra: preprocess instance to finish incomplete jumps

Integer Linear Program Formulation



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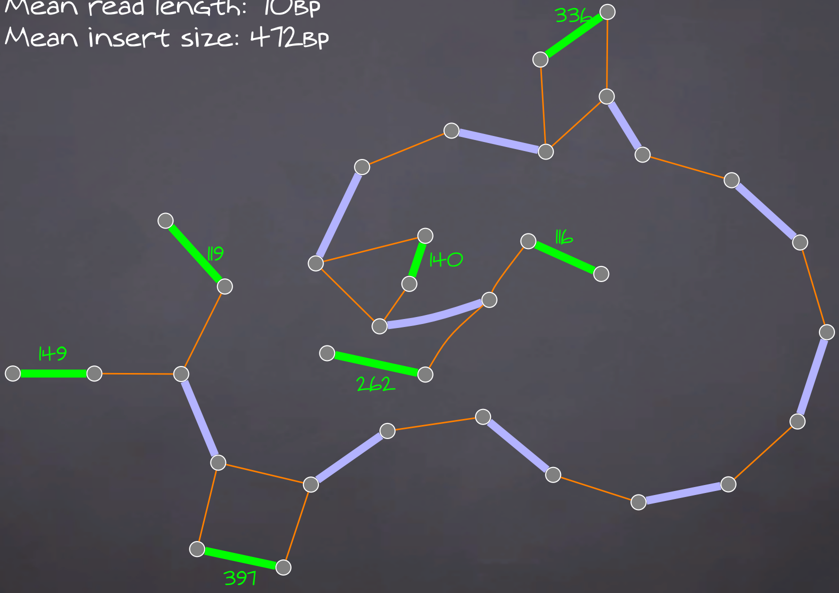

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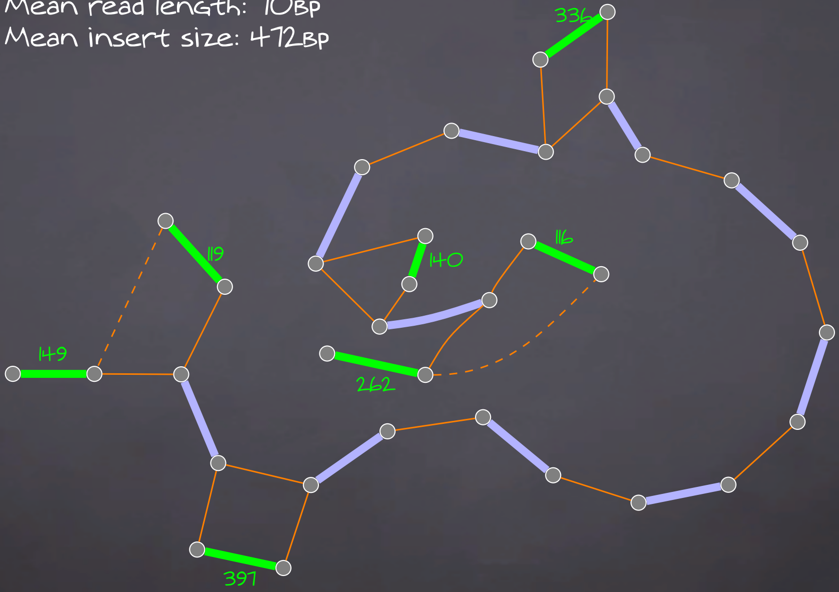

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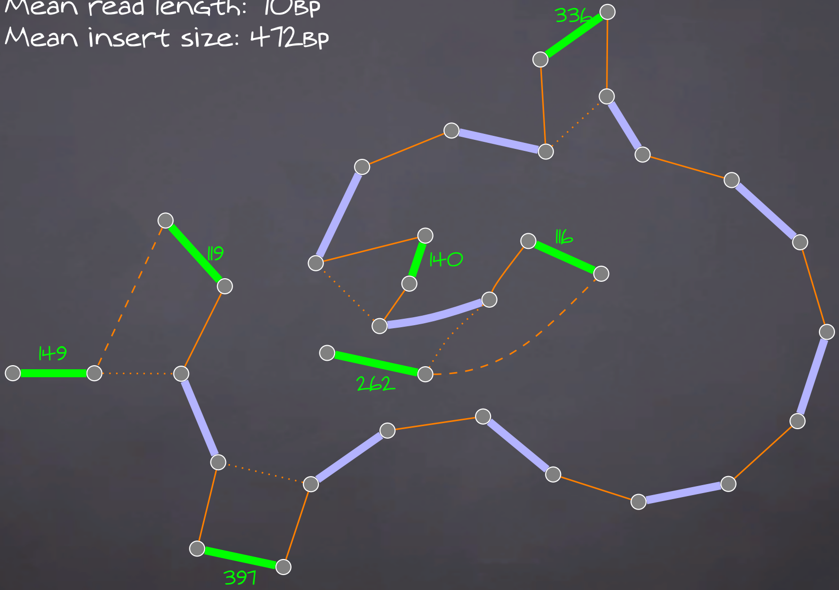
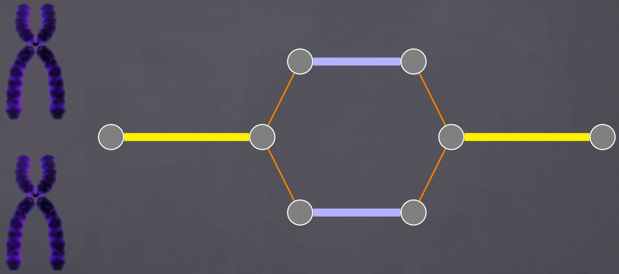


ILP Extension: Multiplicities

GGTGCGAGAGAGGTCATGGATTGCAACGA

GGTGCGAGAGGCCACTCCAATTGCAACGA

ILP Extension: Multiplicities



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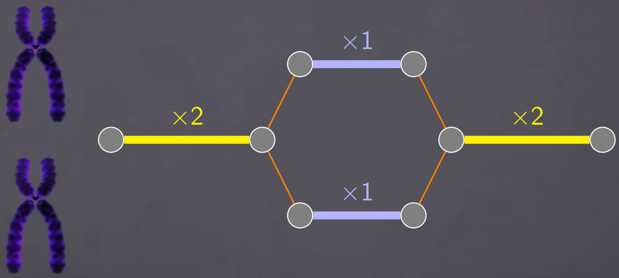

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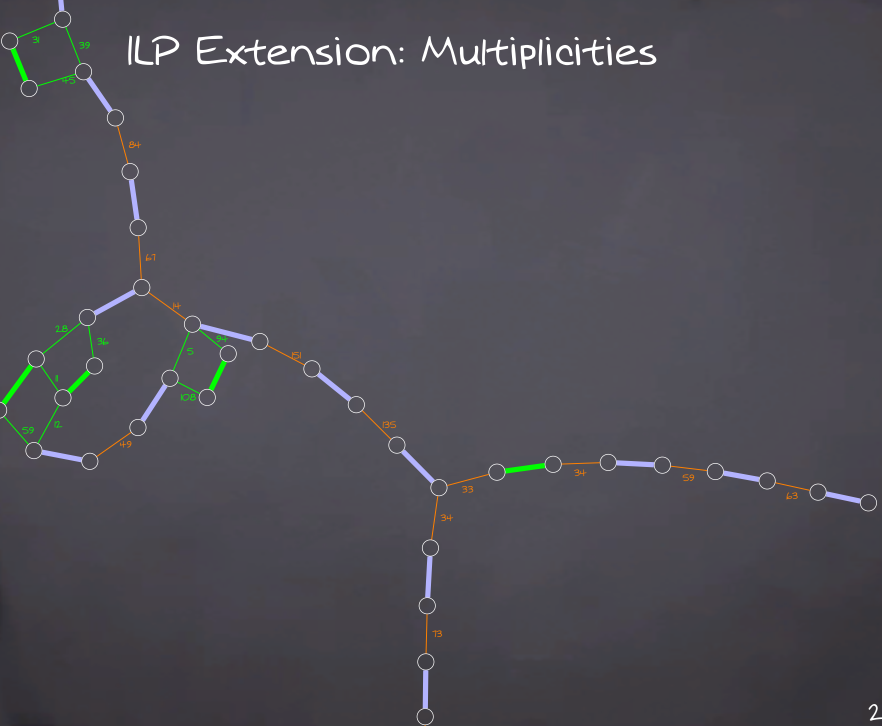

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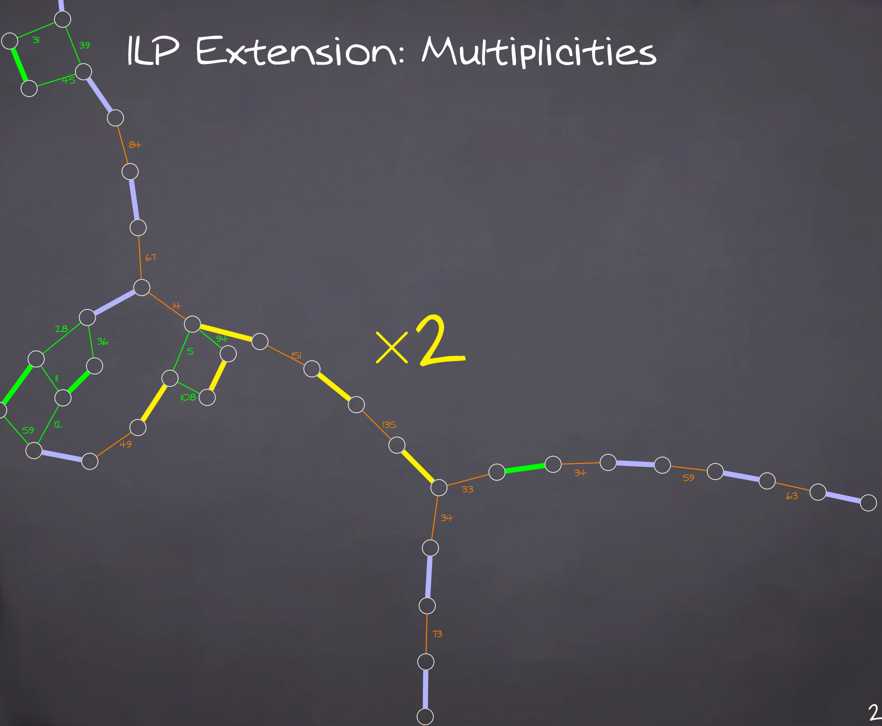
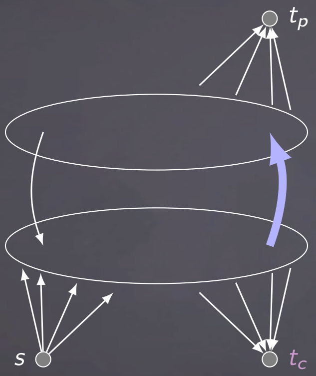


Integer Linear Program Formulation



- chromosomes = disjoint s–$\{t_p, t_c\}$–paths
- bin. variables $y_{uv} = 1 \Leftrightarrow u \to v$ used
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- force contigs: $\forall_{uv \in M} x_{uv} = 1$
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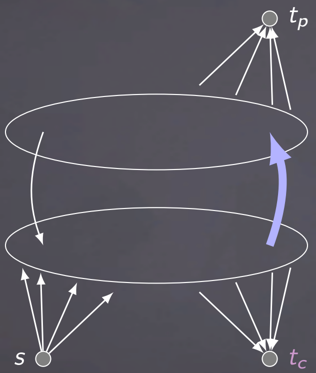
Multiplicities

1. make y_{uv}, $x_{\{u,v\}}$ integers in domain $[0, m(\{u,v\})]$
2. change callback

Integer Linear Program Formulation



- chromosomes = disjoint s–$\{t_p, t_c\}$–paths
- int. variables $y_{uv} = \ell \Leftrightarrow u \to v$ used ℓ times
  $x_{\{u,v\}} = y_{uv} + y_{vu} + z_{uv} + z_{vu}$
- force contigs: $\forall_{uv \in M} x_{uv} \geq 1$
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- forbid cycles (row generation via callback):
  $\forall$ cycle C: $\sum_{uv \in C} y_{uv} \leq |C| \cdot m_{\max} \cdot \sum_{u \in C, v \notin C} y_{uv}$
- objective: $\max \sum_{e \in E} x_{\{u,v\}} \cdot \omega(e)$
- cycle consistency: $\forall_u y_{ut_c} \leq y_{su}$
- jump mechanics !!!

Multiplicities

1. make y_{uv}, $x_{\{u,v\}}$ integers in domain $[0, m(\{u,v\})]$
2. change callback

Linearization of Solutions

Problem

no unique chromosome-configuration explaining solution

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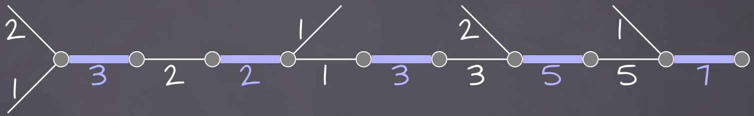

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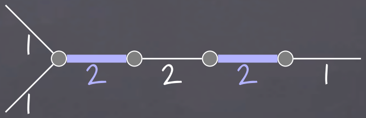
"$\Rightarrow$": contraposition; let $p =$ ambigous path



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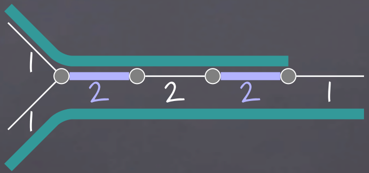

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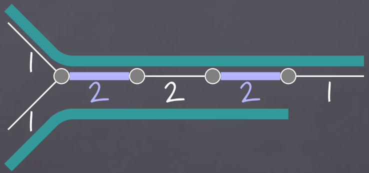

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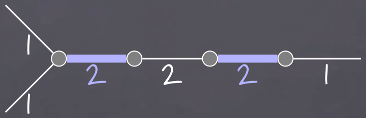

$\rightsquigarrow$ $(G, \mathcal{M}, m)$ not uniquely linearizable

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Reduction (does not decrease number of linearizations):

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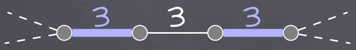

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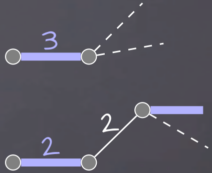

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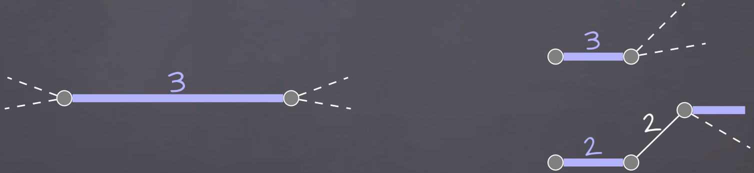

$\rightsquigarrow$ result is collection of alternating paths & cycles

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Linearization of Solutions

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3. cut as few ends as possible

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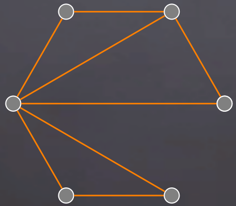

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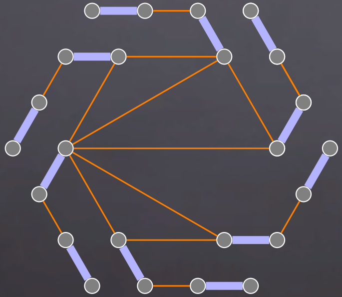

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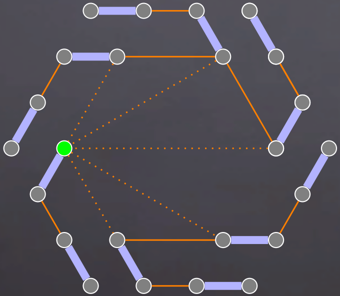

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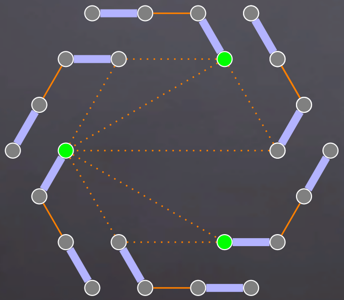

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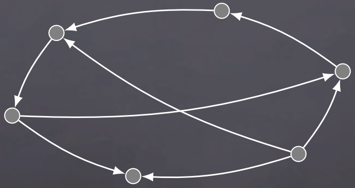

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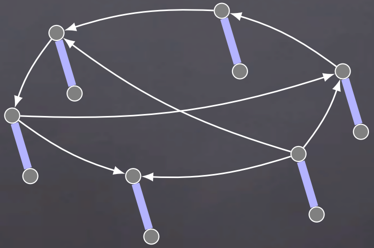

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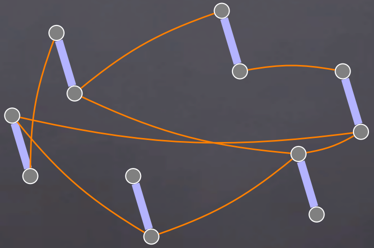

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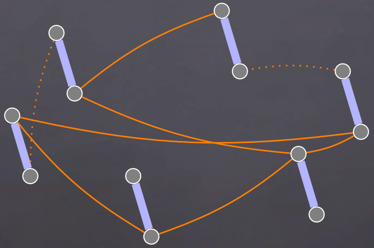

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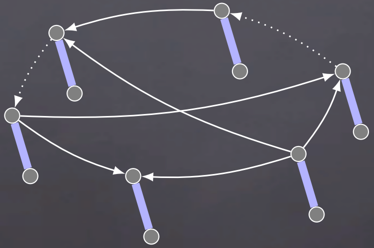

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  2. assemble reads to contigs
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- 3^{rd} generation sequencing: PacBio, Oxford Nanopore produces long reads (10–15kbp), but error-prone
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Fin!