Fast Robinson-Foulds Supertrees
CS598AGB

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Supertree Estimation - combine trees on subsets of data into a single large tree

- Combine sparse scaffold + dense trees on subsets

No discrepancy among true source trees - all disagreement is due to estimation error. This means no ILS, no HGT, etc.
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- Usually doesn't correspond to biological reasons for missing data
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![Diagram](image.png)
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![Phylogenetic inference diagram]

- Source trees
- Supermatrix
- Species
- Computing the species tree
- MRP-Parsimony
- Baum Ragan coding
- MRP matrix
Methods

1. Use species tree estimation methods like ASTRAL, ASTRID, concatenation max-likelihood, concatenated neighbor-joining, etc.
2. Use likelihood, parsimony, etc. on matrix representation (MRP, MRL):
3. Use a heuristic designed for our models of supertrees and source tree error
RF Supertrees

- Exponential decay model of gene tree error (Steel and Rodrigo, 2009)

\[ P_{T,Y}[T'] = \alpha \exp[-\beta RF(T', T|Y)] \]

- The Robinson-Foulds (RF) distance between a binary supertree \( T \) and a binary source tree \( t \) on a taxon subset \( s \) is

\[ RF(T, t) = |\text{bipartitions}(T|_s) \setminus \text{bipartitions}(t)| \]
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- The RF supertree is the tree that minimizes the total RF distance to a set of source trees.
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- The RF supertree is the tree that minimizes the total RF distance to a set of source trees
- The maximum likelihood tree is usually, but not always the RF supertree (depending on \( \alpha \) and \( \beta \) parameters)
Exact Constrained Search with Dynamic Programming

- Theory introduced by Bryant and Steel (2001) for weighted quartet support
  - Input: quartet weights, constraint set $X$
  - Output: species tree constrained by $X$ maximizing induced quartet weight

- Used for minimizing deep coalescences (Than and Nakleh, 2009)
- Used by ASTRAL (Mirarab et al. 2014) and ASTRAL-II (Mirarab and Warnow, 2015) for quartet support

We use an analogous approach for the RF supertree problem
Exact Constrained Search with Dynamic Programming

- Theory introduced by Bryant and Steel (2001) for weighted quartet support
- Used for minimizing deep coalescences (Than and Naklehl, 2009)
  - Input: Cluster compatibility graph from gene trees, constraint set $X$
  - Output: species tree constrained by $X$ minimizing deep coalescences over gene trees
Exact Constrained Search with Dynamic Programming

- Theory introduced by Bryant and Steel (2001) for weighted quartet support
- Used for minimizing deep coalescences (Than and Naklel, 2009)
- Used by ASTRAL (Mirarab et al. 2014) and ASTRAL-II (Mirarab and Warnow, 2015) for quartet support
  - Input: gene trees, constraint set $X$
  - Output: species tree constrained by $X$ maximizing support over gene trees
  - Currently most accurate coalescent-based species tree estimation method
Exact Constrained Search with Dynamic Programming

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Calculating RF support of a supertree

- Suppose a source tree induces the bipartition (on a taxon subset) \{A|B\}
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- A supertree will induce this bipartition if there is some *tripartition* in the supertree that
  1. has every member of \( A \) (and no members of \( B \)) below one child
  2. has at least one member of \( B \) below the other child

![Tree Diagram](image_url)
Calculating RF support of a supertree

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In other words, the single highest edge in the tree that induces \( \{A|B\} \)
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- So we get the RF support of a tripartition in the supertree by counting bipartitions in the input set that correspond to it.
Calculating RF support of a supertree

- So we get the RF support of a tripartition in the supertree by counting bipartitions in the input set that correspond to it.
- Then get the RF support of an entire supertree by adding the RF supports of each tripartition in the tree.
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  1. The weight of the tripartition $ABCD, EFG, HIJ$
  2. The weight of the best subtree on $ABCD$
  3. The weight of the best subtree on $EFG$
- If we have the best subtrees on all subsets, we can try every combination to get the best subtree on $ABCDEF$
Calculating an optimal supertree

For example, to find the optimal subtree on \((abcde)\), we have to try, (among others):

\[\text{optimal subtrees known here} \]

\[(abcde)\]
\[(abcd)(abce)(abde)(acde)(bcde)\]
\[(ab)(ac)(ad)(ae)(bc)(bd)(be)(cd)(ce)(de)\]
\[(a)(b)(c)(d)(e)\]
Running time analysis

- There are $O(2^n)$ possible clades on $n$ taxa
Running time analysis

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- This algorithm takes exponential time
Constrain the search space to avoid exponential time

- Instead of exploring entire search space, only allow trees to contain bipartitions from an input set \( X \)
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- ASTRAL-2 has heuristics to complete trees, then get clades from completed trees
- FastRFS-basic: use ASTRAL-2 clades with DP algorithm
Running time analysis

- $k$ input trees over $n$ taxa: $O(kn)$ input bipartitions
- Checking if tripartition matches bipartition takes $O(n)$ time
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Speed up with precomputation

- Comparing a tripartition against a bipartition takes $O(n)$ time

For each clade $c$, we compute four sets:

1. $c_1$: bipartitions where $c$ contains at least one member of the first half
2. $c_2$: bipartitions where $c$ contains all of the first half
3. $c_3$: bipartitions where $c$ contains at least one member of the second half
4. $c_4$: bipartitions where $c$ contains all of the second half

Then the bipartitions that correspond to a tripartition with children $A_1, A_2$ are the union of $A_1 \cap A_2$, $A_1 \cup A_2$, and $A_1 \cup A_2$.

Precomputation takes $O(|X|^2 n^2 k)$ time; the main phase of the algorithm takes $O(|X|^2 n k)$ time.

Since $|X| \geq n$, the total time for the algorithm is $O(|X|^2 n k)$ (as opposed to $O(|X|^2 n^2 k)$ before).
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Precomputation takes $O(\frac{|X|}{n^2})$ time; the main phase of the algorithm takes $O(\frac{|X|^2}{n^2})$ time.

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- Then the bipartitions that correspond to a tripartition with children $A_1, A_2$ are the union of $A_{11} \cap A_{24}$, $A_{12} \cap A_{23}$, $A_{13} \cap A_{22}$, and $A_{14} \cap A_{21}$
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- Since $|X| \geq n$, the total time for the algorithm is $O(|X|^2nk)$ (as opposed to $O(|X|^2n^2k)$ before)
Improve accuracy of FastRFS

- Sometimes other methods find trees with better RF scores than FastRFS
- If we add that tree to the FastRFS constraint set $X$, we are guaranteed to find a tree at least that good!
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- If we add that tree to the FastRFS constraint set $X$, we are guaranteed to find a tree at least that good!
- FastRFS-enhanced: Add MRL tree to set $X$, and add ASTRID tree if ASTRID is fast
Questions:

1. Can FastRFS find better solutions to the RF supertree problem than other RF supertree heuristics?
2. Does FastRFS-enhanced find better trees than the extra trees we give it?
3. Does FastRFS find trees with good topological accuracy?
4. Is FastRFS faster than heuristic methods?
5. How does FastRFS perform on biological datasets?
Datasets: RF Supertrees

- SMIDgen datasets (Swenson et al., 2010)
  - 100, 500, 1000 species (taxa)
  - Scaffold tree with 20, 50, 75, or 100% of the species
  - 5, 15, or 25 trees with clade-based subsets of species

- Biological datasets

<table>
<thead>
<tr>
<th>Dataset</th>
<th># source trees</th>
<th># taxa</th>
<th>Largest tree</th>
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<tbody>
<tr>
<td>THPL</td>
<td>19</td>
<td>558</td>
<td>140 (25%)</td>
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<tr>
<td>CPL</td>
<td>39</td>
<td>2228</td>
<td>1648 (73%)</td>
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<tr>
<td>Seabirds</td>
<td>7</td>
<td>121</td>
<td>90 (74%)</td>
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<tr>
<td>Marsupials</td>
<td>158</td>
<td>267</td>
<td>267 (100%)</td>
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<tr>
<td>Placental Mammals</td>
<td>726</td>
<td>116</td>
<td>116 (100%)</td>
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FastRFS-basic finds trees with good criterion scores, and FastRFS-enhanced improves them.
FastRFS-basic finds trees with good criterion scores, and FastRFS-enhanced improves them

<table>
<thead>
<tr>
<th>ntaxa</th>
<th>Scaffold %</th>
<th>100</th>
<th>100</th>
<th>100</th>
<th>100</th>
<th>500</th>
<th>500</th>
<th>500</th>
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<td>100</td>
<td>20</td>
<td>50</td>
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<td>31.2</td>
<td>37.8</td>
<td>44.8</td>
<td>170.5</td>
<td>190.4</td>
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<td>414.4</td>
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<td>360.2</td>
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<td>905.0</td>
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<td>2446.6</td>
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<td>29.8</td>
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<td>158.5</td>
<td>178.6</td>
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<td>308.6</td>
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<td>29.2</td>
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<td>30.0</td>
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<td>292.2</td>
<td>346.8</td>
<td>383.8</td>
<td>426.2</td>
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Table 2. Robinson-Foulds Supertree criterion scores on simulated datasets; lower is better. The best result is boldfaced for each model condition. No results are shown for PluMiST and MulRF for the 1000-taxon datasets due to running time limitations for these methods. Results are averaged over ten replicates.
FastRFS finds trees with good criterion scores quickly.

Fig. 4. Scatterplot of normalized Robinson-Foulds Supertree criterion scores (x-axis) and running time (in seconds, y-axis) on the 500-taxon simulated datasets. LEFT: Results shown for all the methods. RIGHT: Results shown only for those methods that obtain good normalized criterion scores (i.e., below 1.2). RF-supertree criterion scores are normalized by the score found by FastMLS-basic, so that values below 1.0 indicate better scores than FastMLS-basic, and values above 1.0 indicate worse scores. The fastest methods are the ones close to the x-axis, but the methods with the best criterion scores are the ones close to the y-axis.
FastRFS almost always finds trees with the lowest topological error

<table>
<thead>
<tr>
<th>ntaxa</th>
<th>100</th>
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<tr>
<td>FastRFS-enhanced</td>
<td>13.3</td>
<td><strong>13.4</strong></td>
<td>10.6</td>
<td>9.3</td>
<td><strong>14.3</strong></td>
<td><strong>13.9</strong></td>
<td><strong>12.0</strong></td>
<td>10.8</td>
<td><strong>16.7</strong></td>
<td><strong>15.1</strong></td>
<td><strong>13.4</strong></td>
<td>11.8</td>
</tr>
</tbody>
</table>

Table 3. Supertree topological error rates on the simulated datasets. The best score for each model condition is boldfaced. No results are shown for PluMiST and MulRF on the 1000-taxon simulated datasets due to running time limitations for these methods. Results are averaged over ten replicates.
FastRFS (quickly) finds good criterion scores on biological data

Fig. 2. Robinson-Foulds Supertree criterion scores on biological data of supertree methods. MulRF and PluMiST could not be run on the CPL dataset, due to its large size; hence no values are shown for those methods on that dataset.

Fig. 3. Sequential running times (in seconds) on biological data of supertree methods. MulRF and PluMiST could not be run on the CPL dataset, due to its large size; hence no values are shown for those methods on that dataset.
FastRFS is fast and accurate

- Finds exact solutions to the RFS problem over a constrained search space
- Faster, more accurate than heuristic searches
- Choice of search space matters!
  - Adding bipartitions from other methods allows finding trees with better criterion score, and frequently better topological error