Intractability of the Minimum-Flip Supertree problem and its variants

Sebastian Böcker\textsuperscript{1}, Quang Bao Anh Bui\textsuperscript{1}, François Nicolas\textsuperscript{1}, and Anke Truss\textsuperscript{1}

Lehrstuhl für Bioinformatik, Friedrich-Schiller-Universität Jena, Ernst-Abbe-Platz 2, Jena, Germany, 
\{sebastian.boecker,quangbaoanh.bui,francois.nicolas,anke.truss\}@uni-jena.de

Abstract. Computing supertrees is a central problem in phylogenetics. The supertree method that is by far the most widely used today was introduced in 1992 and is called Matrix Representation with Parsimony analysis (MRP). Matrix Representation using Flipping (MRF), which was introduced in 2002, is an interesting variant of MRP: MRF is arguably more relevant than MRP and various efficient implementations of MRF have been presented. From a theoretical point of view, implementing MRF or MRP is solving NP-hard optimization problems. The aim of this paper is to study the approximability and the fixed-parameter tractability of the optimization problem corresponding to MRF, namely Minimum-Flip Supertree. We prove strongly negative results.

1 Introduction

When studying the evolutionary relatedness of current taxa, the discovered relations are usually represented as rooted trees, called phylogenies. Phylogenies for various taxa sets are routinely inferred from various kinds of molecular and morphological data sets. A subsequent problem is computing supertrees \cite{1}, i.e., amalgamating phylogenies for non-identical but overlapping taxon sets to obtain more comprehensive phylogenies. Constructing supertrees is easy if no contradictory information is contained in the data \cite{1}. However, incompatible input phylogenies are the rule rather than the exception in practice. The major problem for supertree methods is thus dealing with incompatibilities.

The supertree method that is by far the most widely used today was independently proposed by Baum \cite{3} and Ragan \cite{26} in 1992; it is called Matrix Representation with Parsimony analysis (MRP) \cite{4}. From a theoretical point of view, implementing MRP is designing an algorithm for an NP-hard optimization problem \cite{14,18}, so the running times of MRP algorithms are sometimes prohibitive for large data sets.

In 2002, Chen et al. proposed a variant of MRP \cite{11}, which was later called Matrix Representation using Flipping (MRF) \cite{9}. MRF is arguably more relevant than MRP \cite{4} (see also \cite{12,16}), and various efficient implementations of MRF have been presented \cite{10,13,16}. However, as in the case of MRP, implementing MRF is designing an algorithm for an NP-hard optimization problem \cite{12}, namely MINIMUM-FLIP SUPERTREE. The aim of the present paper is to study the approximability and the fixed-parameter tractability \cite{17} of MINIMUM-FLIP SUPERTREE. We prove strongly negative results.

2 Preliminaries

For each finite set $X$, the cardinality of $X$ is denoted $|X|$. The ring of integers is denoted $\mathbb{Z}$. Define $\overline{\mathbb{Z}} = \mathbb{Z} \cup \{-\infty, +\infty\}$. 
2.1 Rooted phylogenies

Let $S$ be a finite set. A (rooted) phylogeny for $S$ is a subset $T$ of the power set of $S$ that satisfies the following properties: $\emptyset \in T$, $S \in T$, $\{s\} \in T$ for all $s \in S$, and $X \cap Y \in \{\emptyset, X, Y\}$ for all $X, Y \in T$. The elements of $S$ are the leaves of $T$. The elements of $T$ are the clusters of $T$. The most natural representation of $T$ is, of course, a rooted graph-theoretic tree with $|T| - 1$ nodes (the empty cluster does not correspond to any vertex).

Given two phylogenies $T_1$ and $T_2$ for $S$, $T_1$ is a subset of $T_2$ if, and only if, the graph representation of $T_1$ can be obtained from the graph representation of $T_2$ by contracting (internal) edges. If $T_1$ is a subset of $T_2$ and if we assume that hard polytomies never occur then $T_2$ is at least as informative as $T_1$.

2.2 Bipartite graphs and perfect phylogenies

A bipartite graph is a triple $G = (C, S, E)$, where $C$ and $S$ are two finite sets and $E$ is a subset of $C \times S$. The elements of $E$ are the edges of $G$. The elements of $(C \times S) \setminus E$ are the non-edges of $G$. For each $c \in C$, $N_G(c)$ denotes the neighborhood of $c$ in $G$: $N_G(c) = \{s \in S : (c, s) \in E\}$.

Let $M(G)$ denote the set of all quintuples $(s, c, s', c', s'') \in S \times C \times S \times C \times S$ such that $(c, s) \in E$, $(c, s') \in E$, $(c', s') \in E$, $(c', s'') \in E$, $(c, s'') \notin E$, and $(c', s) \notin E$. The latter conditions state that the bipartite graph depicted in [25, Figure 4] is an induced subgraph of $G$. A perfect phylogeny for $G$ is a phylogeny $T$ for $S$ such that $N_G(c)$ is a cluster of $T$ for every $c \in C$. We say that $G$ is M-free [5,11,13,22] (or $\Sigma$-free) [4,9,25] if the following three equivalent conditions are met:

1. for all $c$, $c' \in C$, $N_G(c) \cap N_G(c') \in \{\emptyset, N_G(c), N_G(c')\}$,
2. $M(G)$ is empty, and
3. there is a perfect phylogeny for $G$.

Put $T_G = \{\emptyset, S\} \cup \{N_G(c) : c \in C\} \cup \{\{s\} : s \in S\}$. If $G$ is M-free then $T_G$ satisfies the following two properties:

1. $T_G$ is a perfect phylogeny for $G$.
2. $T_G$ is a subset of any perfect phylogeny for $G$.

Modelization. In our model, $S$ is a set of species (or more generally taxa) and $C$ is a set of binary characters. For each $(c, s) \in C \times S$, $(c, s) \in E$ means that species $s$ possesses character $c$ and $(c, s) \notin E$ means that species $s$ does not possess character $c$. Character data come from the morphological and/or molecular properties of the taxa [21]. The assumption of the model is that for all $c \in C$ and all $s, s' \in S$, the following two assertions are equivalent:

1. Both species $s$ and $s'$ possess character $c$.
2. Some common ancestor of species $s$ and $s'$ possesses character $c$.

A phylogeny for $S$ satisfies the assumption of the model if, and only if, it is a perfect phylogeny for $G$.

2.3 Dealing with incomplete and/or erroneous data sets

A bipartite draft-graph (or weighted bipartite fuzzy graph [6]) is a triple $H = (C, S, F)$, where $C$ and $S$ are two finite sets and $F$ is a function from $C \times S$ to $\mathbb{Z}$. The function $F$ is the weight
function of $H$. The range of $F$ is called the weight range of $H$. An edge of $H$ is an element $e \in C \times S$ such that $F(e) \geq 1$. A joker-edge of $H$ is an element $e \in C \times S$ such that $F(e) = 0$. A non-edge of $H$ is an element $e \in C \times S$ such that $F(e) \leq -1$.

For each $e \in C \times S$, the magnitude of $F(e)$ is the edit cost of $e$ in $H$. An edition of $H$ is a bipartite graph $G$ of the form $G = (C, S, E)$ for some subset $E \subseteq C \times S$. A conflict between $G$ and $H$ is an element $e \in C \times S$ that satisfies one of the following two conditions:

1. $e$ is an edge of $G$ and $e$ is a non-edge of $H$ or
2. $e$ is a non-edge of $G$ and $e$ is an edge of $H$.

The sum of the edit costs in $H$ over all conflicts between $G$ and $H$ is denoted $\Delta(G, H)$:

$$\Delta(G, H) = \sum_{e \in E} \max\{0, -F(e)\} + \sum_{e \in E \setminus (C \times S)} \max\{0, F(e)\}.$$ 

The following minimization problem and its (parameterized) decision version generalize several previously studied problems:

**Name:** Minimum M-Free Edition or Min Edit.
**Input:** A bipartite draft-graph $H$.
**Solution:** An $M$-free edition $G$ of $H$.
**Measure:** $\Delta(G, H)$.

**Name:** M-Free Edition or Edit.
**Input:** A bipartite draft-graph $H$ and an integer $k \geq 0$.
**Question:** Is there an $M$-free edition $G$ of $H$ such that $\Delta(G, H) \leq k$?
**Parameter:** $k$.

For each subset $X \subseteq \mathbb{Z}$, define Min Edit-$X$ as the restriction of Min Edit to those bipartite draft-graphs whose weight ranges are subsets of $X$, and similarly, define Edit-$X$ as the restriction of Edit to those instances $(H, k)$ such that the weight range of $H$ is a subset of $X$. Notably, Min Edit-$\{-1, +1\}$ is the Minimum-Flip Supertree problem and its restriction Min Edit-$\{-1, 0, +1\}$ is the Minimum-Flip Consensus Tree problem [4, 5, 13, 10, 22].

**Modelization.** Incomplete and/or possibly erroneous character data sets are naturally modeled by bipartite draft-graphs: joker-edges represent incompleteness and edit costs allow parsimonious error-corrections.

**Supertrees.** The most interesting feature of Min Edit is that it can be thought as a supertree construction problem, and more precisely, the optimization problem underlying MRF [4, 5, 9, 11, 12].

### 3 Previous results

Min Edit-$X$ has been studied for several subsets $X \subseteq \mathbb{Z}$ [4, 5, 10, 12, 13, 16, 20, 22, 24], sometimes implicitly. Let $H = (C, S, F)$ be a bipartite draft-graph and let $k$ be a non-negative integer.

Put $\mathbb{Z}_+ = \{n \in \mathbb{Z} : n \geq 0\}$ and $\mathbb{Z}_- = \{n \in \mathbb{Z} : n \leq 0\}$. If $H$ has no non-edge, or equivalently, if the weight range of $H$ is a subset of $\mathbb{Z}_+$ then the complete bipartite graph
\(K = (C, S, C \times S)\) is an M-free edition of \(H\) such that \(\Delta(K, H) = 0\). In the same way, if \(H\) has no edge then the empty bipartite graph \(\overline{K} = (C, S, \emptyset)\) is an M-free edition of \(H\) such that \(\Delta(\overline{K}, H) = 0\). Hence, \(\text{MIN EDIT-}Z, \text{ and MIN EDIT-}Z^*\) are trivial problems.

Now, consider the case where the weight range of \(H\) is a subset of \([-\infty, +\infty]\). The bipartite graph
\[
G = (C, S, \{e \in C \times S : F(e) = +\infty\})
\]
is an edition of \(H\) such that \(\Delta(G, H) = 0\); for every edition \(G'\) of \(H\), \(G' \neq G\) implies \(\Delta(G', H) = +\infty\). Therefore, solving \(\text{MIN EDIT on } H\) reduces to deciding whether \(G\) is M-free, which can be achieved in \(O(|C| |S|)\) time \[20\, 21\]. Hence, \(\text{MIN EDIT-}[-\infty, +\infty]\) can be solved in polynomial time because it reduces to the recognition problem associated with the class of M-free bipartite graphs. More generally, \(\text{MIN EDIT-}[-\infty, 0, +\infty]\) can also be solved in polynomial time because it reduces to the sandwich problem \[19\] associated with the class of M-free bipartite graphs: in the case where the weight range of \(H\) is a subset of \([-\infty, 0, +\infty]\), \(\text{MIN EDIT}\) can be solved on \(H\) in \(O(|C| |S|)\) time \[25\].

Put \(I = [-1, +\infty], D = [-\infty, +1]\), and \(U = [-1, +1]\). \(\text{MIN EDIT-I, MIN EDIT-D, and MIN EDIT-U}\) (also known as \(\text{MINIMUM-FLIP CONSENSUS TREE}\)) are the three unweighted edge-modification problems \[24\] associated with the class of M-free bipartite graphs: \(\text{MIN EDIT-I}\) is the insertion (or completion) problem and \(\text{MIN EDIT-D}\) is the deletion problem. \(\text{EDIT-I, EDIT-D, and EDIT-U}\) are NP-complete \[12\].

Put \(\overline{Z} = Z \setminus \{0\}\). \(\text{MIN EDIT-}Z\) is the restriction of \(\text{MIN EDIT}\) to those bipartite draft-graphs that have no joker-edge. The most positive result concerning \(\text{MIN EDIT}\) is that \(\text{EDIT-}Z^\ast\) is FPT: in the case where the weight range of \(H\) is a subset of \(Z^\ast\), deciding whether \(\langle H, k \rangle\) is a yes-instance of \(\text{EDIT}\) (and if so, computing an M-free edition \(G\) of \(H\) such that \(\Delta(G, H) \leq k\)) can be achieved in \(O(6^k |C| |S|)\) time \[12\]. Better FPT algorithms have been presented for the special cases \(\text{MIN EDIT-I}\) \[12\], \(\text{MIN EDIT-D}\) \[12\], and \(\text{MIN EDIT-U}\) \[5\, 22\]. In particular, \(\text{EDIT-U}\) has a polynomial kernel \[22\].

Exact algorithms based Integer Linear Programming \[13\], as well as heuristics \[10\, 16\], have been tested for \(\text{MIN EDIT-}[-1, 0, +1]\) (also known as \(\text{MINIMUM-FLIP SUPERTREE}\)).

4 Contribution

The aim of the present paper is to complete the study of \(\text{MIN EDIT}\) by proving:

**Theorem 1.** For all \(\alpha, \beta \in Z\) such that \(-\alpha < 0 < \beta\) and \((\alpha, \beta) \neq (+\infty, +\infty)\), the following two statements hold:

1. \(\text{EDIT-}[-\alpha, 0, \beta]\) is \(W[2]\)-hard and
2. if there exists a real constant \(\rho \geq 1\) such that \(\text{MIN EDIT-}[-\alpha, 0, \beta]\) is \(\rho\)-approximable in polynomial time then \(P = NP\).

The intractabilities of \(\text{MIN EDIT-}[-1, 0, +\infty]\), \(\text{MIN EDIT-}[-\infty, 0, +1]\), and \(\text{MIN EDIT-}[-1, 0, +1]\) (also known as \(\text{MINIMUM-FLIP SUPERTREE}\)) follow from Theorem 1.

Our proof of Theorem 1 requires the introduction of some material and results from the literature \[8\]. For all \(x, y, z\), let \(\langle x, y|z \rangle\) denote the unique phylogeny for \(\{x, y, z\}\) having \(\{x, y\}\) as a cluster:
\[
\langle x, y|z \rangle = \{\emptyset, \{x\}, \{y\}, \{z\}, \{x, y\}, \{x, y, z\}\}.
\]
A resolved triplet is a phylogeny of the form \( \langle x, y | z \rangle \) for some pairwise distinct \( x, y, z \). Given a phylogeny \( T \) for some superset of \( \{x, y, z\} \), we say that \( \langle x, y | z \rangle \) fits \( T \) if there exists a cluster \( X \) of \( T \) such that \( X \cap \{x, y, z\} = \{x, y\} \).

**Name:** Minimum Resolved Triplets Inconsistency or Min RTI.

**Input:** A finite set \( S \) and a set \( \mathcal{R} \) of resolved triplets with leaves in \( S \).

**Solution:** A phylogeny \( T \) for \( S \).

**Measure:** The number of those elements of \( \mathcal{R} \) that do not fit \( T \).

**Name:** Resolved Triplets Inconsistency or RTI.

**Input:** A finite set \( S \), a set \( \mathcal{R} \) of resolved triplets with leaves in \( S \), and an integer \( k \geq 0 \).

**Question:** Is there a phylogeny \( T \) for \( S \) such that at most \( k \) elements of \( \mathcal{R} \) do not fit \( T \)?

**Parameter:** \( k \).

**Theorem 2** (Byrka, Guillemot, and Jansson 2010 [8]).

1. RTI is \( W[2] \)-hard.
2. If there exists a real constant \( \rho \geq 1 \) such that Min RTI is \( \rho \)-approximable in polynomial time then \( P = NP \).

The idea behind the proof of Theorem 1 is the following: given an instance \((S, \mathcal{R})\) of Min RTI, computing a “good” solution of Min RTI on \((S, \mathcal{R})\) is computing a “good” MRF supertree for the phylogenies in \( \mathcal{R} \).

**Proof (Proof of Theorem 1).** Theorem 1 is deduced from Theorem 2: we show that RTI FPT-reduces to Edit-\(\{−\alpha, 0, \beta\}\). Put \( \gamma = \min\{\alpha, \beta\} \). Note that \( \gamma \) is a positive integer.

Let \((S, \mathcal{R}, k)\) be an arbitrary instance of RTI. The reduction maps \((S, \mathcal{R}, k)\) to an instance \((H, \gamma k)\) of Edit-\(\{−\alpha, 0, \beta\}\), where \( H \) is as follows. Let \( C = \{1, 2, \ldots, |\mathcal{R}|\} \). Write \( \mathcal{R} \) in the form

\[
\mathcal{R} = \{\langle x_c, y_c | z_c \rangle : c \in C\}.
\]

Let \( F \) be the function from \( C \times S \) to \( \mathbb{Z} \) given by:

\[
F(c, s) = \begin{cases} 
\beta & \text{if } s \in \{x_c, y_c\} \\
0 & \text{if } s \notin \{x_c, y_c, z_c\} \\
-\alpha & \text{if } s = z_c
\end{cases}
\]

for all \((c, s) \in C \times S\). Let \( H = (C, S, F) \).

Clearly \((H, \gamma k)\) is computable from \((S, \mathcal{R}, k)\) in polynomial time. It remains to prove that \((S, \mathcal{R}, k)\) is a yes-instance of RTI if, and only if, \((H, \gamma k)\) is a yes-instance of Edit.

**If:** Assume that \((H, \gamma k)\) is a yes-instance of Edit. Then, there exists an \( M \)-free edition \( G \) of \( H \) such that \( \Delta(G, H) \leq \gamma k \). Let \( C' \) denote the set of all \( c \in C \) such that \((c, s)\) is a conflict between \( G \) and \( H \) for at least one \( s \in \{x_c, y_c, z_c\} \). Since there are at least \(|C'|\) conflicts between \( G \) and \( H \), we have \( \gamma |C'| \leq \Delta(G, H) \), and thus \(|C'| \leq k \). Let \( T \) be a perfect phylogeny for \( G \). For each \( c \in C \setminus C' \), we have \( N_{C'}(c) \cap \{x_c, y_c, z_c\} = \{x_c, y_c\} \), and thus \( \langle x_c, y_c | z_c \rangle \) fits \( T \). Hence, \( T \) is a phylogeny for \( S \) such that at most \( k \) elements of \( \mathcal{R} \) do not fit \( T \). Therefore, \((S, \mathcal{R}, k)\) is a yes-instance of RTI.
Only if. Assume that \((S, R, k)\) is a yes-instance of RTI. Then, there exists a phylogeny \(T\) for \(S\) such that at most \(k\) elements of \(R\) do not fit \(T\). Let \(C'\) denote the set of all \(c \in C\) such that \(\{x_c, y_c, z_c\}\) does not fit \(T\). For each \(c \in C \setminus C'\), let \(X_c\) be a cluster of \(T\) such that 
\[X_c \cap \{x_c, y_c, z_c\} = \{x_c, y_c\}.\]
If \(\alpha \leq \beta\) then let \(X_c = S\) for each \(c \in C'\); if \(\beta < \alpha\) then let \(X_c = \{x_c\}\) for each \(c \in C'\). Put \(G = (C, S, \bigcup_{c \in C}\{e \times X_c\}).\)

1. \(G\) is an edition of \(H\).
2. \(T\) is a perfect phylogeny for \(G\) because \(N_G(c) = X_c\) is a cluster of \(T\) for all \(c \in C\).
3. Let \(\Gamma\) denote the set of all conflicts between \(G\) and \(H\). If \(\alpha \leq \beta\) then \(\Gamma = \{(c, z_c) : c \in C'\};\)
if \(\beta < \alpha\) then \(\Gamma = \{(c, y_c) : c \in C'\}\). The edit cost in \(H\) of every conflict between \(G\) and \(H\) equals \(\gamma\). Therefore, we have 
\[\Delta(G, H) = \gamma |\Gamma| = \gamma |C'| \leq \gamma k.\]

Hence, \((H, \gamma k)\) is a yes-instance of EDIT.

Proof (Proof of Theorem 1.2.). Let \(\rho\) be real number greater than or equal to 1. It follows from the proof of Theorem 1.1 that if \(G\) is a \(\rho\)-approximate solution of Min Edit on \(H\) then any perfect phylogeny for \(G\) is a \(\rho\)-approximate solution of Min RTI on \((S, R)\). Therefore, if Min Edit is \(\rho\)-approximable in polynomial time then Min RTI is also \(\rho\)-approximable in polynomial time. It is now clear that Theorem 1.2 follows from Theorem 2.2.

5 Conclusion

To conclude, let us contrast Theorem 1.2 with two recent results.

The Maximum Parsimony (MP) problem [2] is the NP-hard optimization problem [14,18] underlying MRP, as Min Edit is the optimization problem underlying MRF. Although Min Edit is NP-hard to approximate within any constant factor by Theorem 1.2, MP is 1.55-approximable in polynomial time [2].

The parameterized problems Edit and Weighted Fuzzy Cluster Editing (WFCE) [3] are closely related: WFCE is the draft-graph edition problem corresponding to the class of \(P_3\)-free graphs. Edit is \(W[2]\)-hard by Theorem 1.1 but WFCE has been recently shown to be fixed-parameter tractable [23] (see also [7,15]).

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