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# A simple characterization of the minimal obstruction sets for three-state perfect phylogenies

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ABSTRACT

We give a characterization of the minimal obstruction sets for the existence of a perfect phylogeny for a set of three-state characters that can be inferred by testing each pair of characters. This leads to a $O(m^2n + p)$ time algorithm for outputting all $p$ minimal obstruction sets for a set of $m$ three-state characters over a set of $n$ taxa.



## 1. Introduction

The *k-state perfect phylogeny problem* is a classic problem in computational biology [1]. The input is an $n$ by $m$ matrix $\mathcal{M}$ of integers from the set $K = \{1, \ldots, k\}$. We refer to each row of $\mathcal{M}$ as a *taxon* (plural *taxa*), each column of $\mathcal{M}$ as a *character*, and each value that occurs in a column $c$ of $\mathcal{M}$ as a *state* of character $c$. A *perfect phylogeny* for $\mathcal{M}$ is a tree $T$ with $n$ leaves such that each leaf is labeled by a distinct taxon of $\mathcal{M}$, each internal node is labeled by a vector in $K^m$, and, for every character $c$ and every state $i$ of $c$, the nodes labeled with state $i$ for character $c$ form a connected subtree of $T$. The problem is to decide whether there exists a perfect phylogeny for $\mathcal{M}$. If so, then the characters of $\mathcal{M}$ are *compatible*. Otherwise, they are *incompatible*. The general $k$-state perfect phylogeny problem is NP-complete [2,3]. However, for fixed $k$, the problem is solvable in $O(m^2n)$ time [4,5], and in $O(mn)$ time when $k = 2$ [6].

In this note, we focus on the three-state perfect phylogeny problem, and thus, fix $\mathcal{M}$ to be an $n$ by $m$ matrix of integers from the set $\{1, 2, 3\}$. We remark that several specialized algorithms have been developed for the specific case where $k = 3$ that can construct a perfect phylogeny for $\mathcal{M}$ (when one exists) in $O(m^2n)$ time [7–11]. However, our main concern here is the case where the characters of $\mathcal{M}$ are incompatible. Since every subset of a compatible set of characters is compatible, it follows that if the characters of $\mathcal{M}$ are incompatible, there must be some minimal subset of the characters of $\mathcal{M}$ that are incompatible. A *minimal obstruction set* for $\mathcal{M}$ is a minimal subset of the characters of $\mathcal{M}$ that are incompatible. A recent breakthrough [12] showed that every minimal obstruction set for $\mathcal{M}$ has cardinality at most 3; implying an $O(m^3n)$ time algorithm for outputting all minimal obstruction sets for $\mathcal{M}$. The main result of this work is a characterization of the minimal obstruction sets for $\mathcal{M}$ that can be inferred by testing each pair of the characters of $\mathcal{M}$. We show that this leads to a $O(m^2n+p)$ time algorithm for outputting all $p$ minimal obstruction sets for $\mathcal{M}$. Although there can be $O(m^3)$ minimal obstruction sets for $\mathcal{M}$, in practice we expect the number of minimal obstruction sets to be small.

We conclude with a theorem relating our characterization of the minimal obstruction sets for three-state perfect phylogenies to monochromatic pairs of vertices of the partition intersection graph of $\mathcal{M}$ with no legal minimal separator. By the results of [10–12] the existence of such a pair of vertices certifies that no perfect phylogeny for $\mathcal{M}$ exists.

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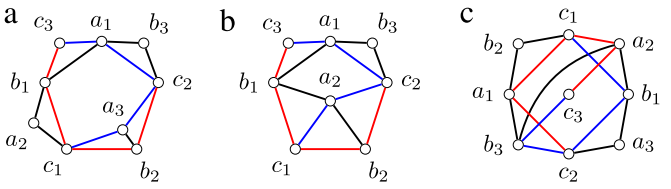


**Fig. 1.** The "forbidden" sets of edges in the intersection graph of three three-state characters that admit a perfect phylogeny. In [12], four forbidden subgraphs are given. However, one of the subgraphs given is a subgraph of another. For our purposes, the supergraph is not needed and so it is not shown here. The colored edges are used in the proof of Theorem 6.

## 2. Preliminaries

We fix $\mathcal{M}$ to be an $n$ by $m$ matrix of integers from the set $\{1, 2, 3\}$. For a subset $C$ of the characters of $\mathcal{M}$, the matrix $\mathcal{M}|C$ is obtained by restricting $\mathcal{M}$ to the characters in $C$. $\mathcal{G}(\mathcal{M})$ is the *intersection graph* of $\mathcal{M}$ which has a vertex $c_i$ for each character $c$ of $\mathcal{M}$ and each state $i$ of $c$, and an edge $c_i d_j$ precisely when there is a taxon of $\mathcal{M}$ having state $i$ for character $c$ and state $j$ for character $d$. Note that $\mathcal{G}(\mathcal{M})$ cannot have an edge between vertices associated with different states of the same character of $\mathcal{M}$.

In [7], a matrix $\overline{\mathcal{M}}$ of two-state characters is derived from $\mathcal{M}$ by adding, for each character $c$ of $\mathcal{M}$, two-state characters $c(1), c(2), c(3)$ to $\overline{\mathcal{M}}$. All taxa having state $i$ for $c$ are given state 1 for $c(i)$, and all other taxa are given state 2 for $c(i)$. Since every character of $\overline{\mathcal{M}}$ has two states, it follows from the splits equivalence theorem (also known as the four-gamete condition) that two characters $c(i)$ and $d(j)$ of $\overline{\mathcal{M}}$ are *incompatible* if and only if the two columns corresponding to $c(i)$ and $d(j)$ contain all four of the pairs $(1, 1), (1, 2), (2, 1)$, and $(2, 2)$; otherwise $c(i)$ and $d(j)$ are *compatible* [13]. Note that this implies that $c(i)$ and $d(j)$ are compatible if and only if $\mathcal{G}(\overline{\mathcal{M}}|\{c(i), d(j)\})$ is not a cycle. A set of two-state characters is compatible if and only if each pair of characters in the set is compatible [13]. Theorem 1 shows that we can test for the existence of a perfect phylogeny for $\mathcal{M}$ by finding a compatible subset of the characters in $\overline{\mathcal{M}}$.

**Theorem 1** (*See [7]*)**.** *There is a perfect phylogeny for $\mathcal{M}$ if and only if there is a subset $C$ of the characters in $\overline{\mathcal{M}}$ such that both of the following hold:* (i) *every pair of characters in $C$ is compatible; and* (ii) *for every character $c$ of $\mathcal{M}$, $C$ contains at least two characters from the set $\{c(1), c(2), c(3)\}$.*

Theorem 2 generalizes the splits equivalence theorem to three-state characters.

**Theorem 2** (*See [12]*)**.** *There is a perfect phylogeny for $\mathcal{M}$ if and only if both of the following hold:* (i) *for every pair $\{a, b\}$ of characters of $\mathcal{M}$, $\mathcal{G}(\mathcal{M}|\{a, b\})$ is acyclic; and* (ii) *for every triple $\{a, b, c\}$ of characters of $\mathcal{M}$, $\mathcal{G}(\mathcal{M}|\{a, b, c\})$ does not contain, up to relabeling of characters and states, any of the subgraphs shown in Fig 1.*

## 3. The main results

For a character $c$ of $\mathcal{M}$ and a state $i$ of $c$, if there is a character $d$ of $\mathcal{M}$ and two states $j$ and $k$ of $d$ such that $c(i)$ is incompatible with both $d(j)$ and $d(k)$, then we say that $i$ is a *dependent* state of $c$ with $d$ as a *witness*. We give a complete characterization of the obstruction sets for $\mathcal{M}$ in terms of the dependent states of its characters.

**Lemma 3.** *Let $c$ be a character of $\mathcal{M}$ and let $i$ be a dependent state of $c$. No subset of the characters in $\overline{\mathcal{M}}$ satisfying both conditions* (i) *and* (ii) *of Theorem 1 contains $c(i)$.*

**Proof.** Let $C$ be a subset of the characters of $\overline{\mathcal{M}}$ containing $c(i)$. Since $i$ is a dependent state, there is a character $d$ of $\mathcal{M}$ and two states $j, k$ of $d$ such that $c(i)$ is incompatible with both $d(j)$ and $d(k)$. It follows that either $C$ contains at most one of $\{d(1), d(2), d(3)\}$, or $C$ contains a pair of incompatible characters. Thus, $C$ cannot satisfy both conditions (i) and (ii) of Theorem 1. □

**Theorem 4.** *Let $a$, $b$, and $c$ be three characters of $\mathcal{M}$ where $c$ has two dependent states $i$ and $j$ such that $a$ is a witness that state $i$ is dependent, and $b$ is a witness that state $j$ is dependent. The set $\{a, b, c\}$ is an obstruction set for $\mathcal{M}$. Furthermore, if the characters in $\{a, b, c\}$ are pairwise compatible, then $\{a, b, c\}$ is a minimal obstruction set for $\mathcal{M}$.*

**Proof.** Let $M = \mathcal{M}|\{a, b, c\}$ and suppose that $C$ is a subset of the characters in $\overline{M}$ satisfying both conditions (i) and (ii) of Theorem 1. By Lemma 3, $c(i) \notin C$ and $c(j) \notin C$. Then $C$ contains at most one of $\{c(1), c(2), c(3)\}$. This contradicts that $C$ satisfies condition (ii) of Theorem 1. Hence, no such $C$ exists. So by Theorem 1, there is no perfect phylogeny for $M$ and $\{a, b, c\}$ is an obstruction set for $\mathcal{M}$. □

We now give a characterization of when a state is dependent using the intersection graph of two characters of $\mathcal{M}$, and then show that every minimal obstruction set for $\mathcal{M}$ contains a character with two dependent states. For a path $p : p_1p_2p_3p_4p_5$ of length 4, we write mid$(p)$ to denote $p_3$, the "middle" vertex of $p$. We consider a 4-cycle to be a path of length 4 and mid$(p)$ is allowed to be any vertex on the cycle. Note that at least four vertices lie on any cycle in $\mathcal{G}(\mathcal{M})$, and for a pair $\{c, d\}$ of characters of $\mathcal{M}$, every state associated with a vertex on a cycle in $\mathcal{G}(\mathcal{M}|\{c, d\})$ is dependent.

**Lemma 5.** *A state $i$ of a character $c$ of $\mathcal{M}$ is a dependent state if and only if there is a character $d$ of $\mathcal{M}$ and a path $p$ of length 4 in $\mathcal{G}(\mathcal{M}|\{c, d\})$ with $c_i = \text{mid}(p)$. Furthermore, if such a $d$ exists, then $d$ is a witness that $i$ is a dependent state of $c$.*

**Proof.** ($\Rightarrow$) Suppose that $i$ is a dependent state of a character $c$ of $\mathcal{M}$ with $d$ as witness. W.l.o.g. relabel the states of $c$ and $d$ so that $i = 1$ and that $c(1)$ is incompatible with both $d(1)$ and $d(2)$. Let $G = \mathcal{G}(\mathcal{M}|\{c, d\})$. Then, $c_1d_1$ and $c_1d_2$ are edges of $G$. Since, $c(1)$ is incompatible with $d(1)$, either $c_2d_1$ or $c_3d_1$ is an edge of $G$. Since $c(1)$ is incompatible with $d(2)$, either $c_2d_2$ or $c_3d_2$ is an edge of $G$. We show that in every case $G$ contains a path $p$ such that $\text{mid}(p) = c_1$. If $c_2d_1$ and $c_2d_2$ are edges of $G$, then $c_1d_1c_2d_2c_1$ is a cycle containing $c_1$. If $c_2d_1$ and $c_3d_2$ are edges of $G$, then $c_3d_2c_1d_1c_2$ is the required path of length 4. If $c_3d_1$ and $c_2d_2$ are edges of $G$, then $c_2d_2c_1d_1c_3$ is the required path of length 4. If $c_3d_1$ and $c_3d_2$ are edges of $G$, then $c_1d_1c_3d_2c_1$ is a cycle containing $c_1$. ($\Leftarrow$) Let $d$ be a character of $\mathcal{M}$ such that there is a path $p$ of length 4 in $G = \mathcal{G}(\mathcal{M}|\{c, d\})$ with $c_i = \text{mid}(p)$. W.l.o.g. relabel the states of $c$ and $d$ so that $i = 1$. $G$ cannot contain edges between two states of the same character. So either $p$ is a cycle containing $c_1$, or the path $c_2d_1c_1d_2c_3$ (up to possibly renaming states $d_1$ and $d_2$). In both cases, the four-gamete condition shows that $c(1)$ is incompatible with two of $d(1)$, $d(2)$, $d(3)$. Hence, state 1 is a dependent state of $c$ with $d$ as witness. □

**Theorem 6.** *Let $C$ be a minimal obstruction set for $\mathcal{M}$. Then $C$ contains a character with two dependent states.*

**Proof.** By Theorem 2, the cardinality of $C$ is either 2 or 3. *Case* 1. If the cardinality of $C$ is 2, then it follows from Theorem 2 that $\mathcal{G}(\mathcal{M}|C)$ contains a cycle. Since there cannot be an edge in $\mathcal{G}(\mathcal{M}|C)$ between vertices associated with states of the same character, it follows that any cycle $\mathcal{G}(\mathcal{M}|C)$ has at least four vertices, and every state associated with a vertex on this cycle is a dependent state. The theorem follows. *Case* 2. If the cardinality of $C$ is 3, then it follows from Theorem 2 that $\mathcal{G}(\mathcal{M}|C)$ contains one of the graphs of Fig 1 as a subgraph (after possibly renaming the characters and states of $\mathcal{M}|C$). If Fig 1(a) is a subgraph of $\mathcal{G}(\mathcal{M}|C)$, then $c_3b_1c_1b_2c_2$ (colored red) is a path showing that state 1 of $c$ is dependent, and $c_3a_1c_2a_3c_1$ (colored blue) is a path showing that state 2 of $c$ is dependent. If Fig 1(b) is a subgraph of $\mathcal{G}(\mathcal{M}|C)$, then $c_3b_1c_1b_2c_2$ (colored red) is a path showing that state 1 of $c$ is dependent, and $c_3a_1c_2a_2c_1$ (colored blue) is a path showing that state 2 of $c$ is dependent. If Fig 1(c) is a subgraph of $\mathcal{G}(\mathcal{M}|C)$, then $c_3a_2c_1a_1c_2$ (colored red) is a path showing that state 1 of $c$ is dependent, and $c_3b_3c_2b_1c_1$ (colored blue) is a path showing that state 2 of $c$ is dependent. In every case, we have shown that states 1 and 2 are dependent states of $c$. Thus, $\mathcal{M}$ contains a character with two dependent states. □

Theorems 4 and 6 together with Theorem 2 give us the following test for the existence of a perfect phylogeny for $\mathcal{M}$.

**Theorem 7.** *There is a perfect phylogeny for $\mathcal{M}$ if and only if there is at most one dependent state of each character $c$ of $\mathcal{M}$.*

**Proof.** If there is a perfect phylogeny for $\mathcal{M}$, then there is no obstruction set for $\mathcal{M}$. Thus, by Theorem 4, there can be no character of $\mathcal{M}$ with more than one dependent state. If there is no perfect phylogeny for $\mathcal{M}$, then there must exist some minimal obstruction set for $\mathcal{M}$. By Theorem 6, there is a character of $\mathcal{M}$ with two or more dependent states. □

An immediate consequence of Theorem 7 is that every set $C$ of three-state characters has a canonical subset that *does* have a perfect phylogeny, namely the subset $\{c \in C : c \text{ has at most one dependent state}\}$.

We now describe an algorithm, denoted by $\mathcal{A}$, which outputs all of the minimal obstruction sets for $\mathcal{M}$. Step 1 of $\mathcal{A}$ computes for each character $c$ of $\mathcal{M}$ the following.

- A set $\mathcal{B}(c)$ of all characters $d$ of $\mathcal{M}$ such that $\mathcal{G}(\mathcal{M}|\{c, d\})$ contains a cycle.
- For each state $i$ of $c$, a set $\mathcal{D}(c, i)$ of all characters $d$ of $\mathcal{M}$ such that $d \notin \mathcal{B}(c)$ and there is a path $p$ of length 4 in $\mathcal{G}(\mathcal{M}|\{c, d\})$ with $c_i = \text{mid}(p)$.

Step 2 of $\mathcal{A}$ visits each character $c$ of $\mathcal{M}$ and outputs the following.

- For each character $d$ in $\mathcal{B}(c)$, the set $\{c, d\}$.
- For each pair of states $\{i, j\}$ of $c$ with both $\mathcal{D}(c, i)$ and $\mathcal{D}(c, j)$ non-empty, each element of the set $\{\{c, x, y\} : x \in \mathcal{D}(c, i), y \in \mathcal{D}(c, j)\}$.

**Theorem 8.** *$\mathcal{A}$ outputs all $p$ minimal obstruction sets for $\mathcal{M}$ in $O(m^2n + p)$ time.*

**Proof.** We first establish the following claim.

**Claim 1.** *For each character $c$ of $\mathcal{M}$, the sets $\mathcal{B}(c)$, $\mathcal{D}(c, 1)$, $\mathcal{D}(c, 2)$, and $\mathcal{D}(c, 3)$ are pairwise disjoint.*

**Proof of Claim 1.** Clearly $\mathcal{B}(c) \cap (\mathcal{D}(c, 1) \cup \mathcal{D}(c, 2) \cup \mathcal{D}(c, 3)) = \emptyset$, so it suffices to show that for each character $c$ of $\mathcal{M}$, the sets $\mathcal{D}(c, 1)$, $\mathcal{D}(c, 2)$, and $\mathcal{D}(c, 3)$ are pairwise disjoint. W.l.o.g. let $c$ be a character of $\mathcal{M}$ and let $d \in \mathcal{D}(c, 1) \cap \mathcal{D}(c, 2)$. Let $G = \mathcal{G}(\mathcal{M}|\{c, d\})$. Since $d \in \mathcal{D}(c, 1) \cap \mathcal{D}(c, 2)$, $d \notin \mathcal{B}(c)$, and there are paths $p_1$ and $p_2$ of length 4 in $G$ with $c_1 = \text{mid}(p_1)$ and $c_2 = \text{mid}(p_2)$. Since $d \notin \mathcal{B}(c)$, $G$ is acyclic. W.l.o.g. suppose that $p_1$ is the path $c_2d_1c_1d_2c_3$. Since $\text{mid}(p_2) = c_2$, there must be two edges from $c_2$ to vertices associated with states of $d$. We have that $c_2d_1$ is an edge of $p_1$. If $c_2d_2$ is an edge of $p_2$, then we have a cycle in $G$. So $c_2d_3$ and either $d_3c_3$ or $d_3c_1$ are edges of $p_2$. In either case, there is a cycle in $G$. □

By Lemma 5, $\mathcal{A}$ finds all dependent states, and hence, by Theorems 2, 4 and 6, outputs all of the minimal obstruction sets for $\mathcal{M}$. By Claim 1, every obstruction set output by $\mathcal{A}$ is minimal. We now establish the runtime. Step 1 of $\mathcal{A}$ takes $O(m^2n)$ time to construct the intersection graphs of each pair of characters of $\mathcal{M}$. Since each intersection graph has exactly six vertices and at most nine edges, it follows that it all cycles and paths of length 4 can be found in $O(1)$ time. Hence step 1 takes $O(m^2n)$ time. Step 2 of $\mathcal{A}$ visits each of the $m$ characters of $\mathcal{M}$ and takes $O(1)$ time per set output. Any minimal obstruction set of cardinality 2 will be output twice. If follows from Claim 1 that each minimal obstruction set of cardinality 3 will be output at most three times. Thus, step 2 takes $O(m + p)$ time where $p$ is the number of minimal obstruction sets. Hence, $\mathcal{A}$ takes $O(m^2n + p)$ time to complete both steps 1 and 2. □

Several approaches to determining the existence of a perfect phylogeny for $\mathcal{M}$ studied in the literature make use of separating sets in $\mathcal{G}(\mathcal{M})$ [10,11]. For two vertices $a$ and $b$ of $\mathcal{G}(\mathcal{M})$, an *a–b separator* is a set of vertices whose removal separates $a$ from $b$. An $a$–$b$ separator is *minimal* if no subset of it is an $a$–$b$ separator. A *minimal separator* is a separator that is a minimal $a$–$b$ separator for some pair $a$, $b$ of vertices of $\mathcal{G}(\mathcal{M})$. A minimal separator $S$ of $\mathcal{G}(\mathcal{M})$ is *legal* if, for each character $c$ of $\mathcal{M}$, $S$ contains at most one vertex corresponding to a state of $c$. A pair of vertices of $\mathcal{G}(\mathcal{M})$ representing different states of the same character is *monochromatic*.

**Theorem 9** (*See [10–12]*)**.** *There is a perfect phylogeny for $\mathcal{M}$ if and only if both of the following hold:* (i) *the characters of $\mathcal{M}$ are pairwise compatible; and* (ii) *every monochromatic pair of vertices in $\mathcal{G}(\mathcal{M})$ is separated by a legal minimal separator.*

We conclude with Theorem 10 that relates dependent states to legal minimal separators. A consequence of Theorem 10 is that algorithm $\mathcal{A}$ can be easily modified to output monochromatic pairs of vertices of $\mathcal{G}(\mathcal{M})$ with no legal minimal separator.

**Theorem 10.** *Suppose that the characters of $\mathcal{M}$ are pairwise compatible. Two states $i$ and $j$ of a character $c$ of $\mathcal{M}$ are dependent if and only if there is no legal minimal separator for $c_i$ and $c_j$ in $\mathcal{G}(\mathcal{M})$.*

**Proof.** By Theorems 2 and 9, it suffices to show that the theorem holds for every minimal obstruction set, i.e., for each graph in Fig 1, a monochromatic pair of vertices has no legal minimal separator if and only if they correspond to a pair of dependent states. This is verified by inspection. In the graph of Fig 1(a): $\{c_1, c_2\}$ is the only *monochromatic* pair of vertices with no legal minimal separator; 3 is the only dependent state of $a$; 2 is the only dependent state of $b$; and 1 and 2 are the only dependent states of $c$. In the graph of Fig 1(b): $(b_1, b_2)$ and $(c_1, c_2)$ are the only monochromatic pairs of vertices with no legal minimal separator; there are no dependent states of $a$; 1 and 2 are the only dependent states of $b$; and 1 and 2 are the only dependent states of $c$. In the graph of Fig 1(c): $(a_1, a_2)$, $(b_1, b_3)$, $(c_1, c_2)$, and are the only monochromatic pairs of vertices with no legal minimal separator; 1 and 2 are the only dependent states of $a$; 1 and 3 are the only dependent states of $b$; and 1 and 2 are the only dependent states of $c$. □

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