Unique Perfect Phylogeny Characterizations via Uniquely Representable Chordal Graphs

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Abstract. The perfect phylogeny problem is a classic problem in computational biology, where we seek an unrooted phylogeny that is compatible with a set of qualitative characters. Such a tree exists precisely when an intersection graph associated with the character set, called the partition intersection graph, can be triangulated using a restricted set of fill edges. Semple and Steel used the partition intersection graph to characterize when a character set has a unique perfect phylogeny. Bordewich, Huber, and Semple showed how to use the partition intersection graph to find a maximum compatible set of characters. In this paper, we build on these results, characterizing when a unique perfect phylogeny exists for a subset of partial characters. Our characterization is stated in terms of minimal triangulations of the partition intersection graph that are uniquely representable, also known as ur-chordal graphs. Our characterization is motivated by the structure of ur-chordal graphs, and the fact that the block structure of minimal triangulations is mirrored in the graph that has been triangulated.

1 Introduction

An $X$–tree is a pair $T_x = (T, \phi)$ where $T$ is a tree and $\phi$ is a map from $X$ to the nodes of $T$, such that every node of $T$ with degree two or one is mapped to by $\phi$. We will call the range of $\phi$ the labeled nodes of $T_x$, and these nodes are labeled by $\phi$. The underlying tree of $T_x$ is $T$. An $X$–tree is free if $\phi$ is a bijection to the leaves of $T$, and it is ternary if every internal node of $T$ has degree three. Given $A \subseteq X$, we will use $T_x(A)$ to denote the minimal subtree of $T$ containing the nodes $\phi(A)$. Two subtrees $T_x(A)$ and $T_x(A')$ of $T$ intersect if they have one or more nodes in common, and if $v$ is a common node of $T_x(A)$ and $T_x(A')$ we say that $T_x(A)$ and $T_x(A')$ intersect at $v$.

A partial character for $X$ is a partition $\chi = A_1 | A_2 | \ldots | A_r$ of a subset $X' \subseteq X$. Each $A_i$ is called a cell of $\chi$. If $T_x(A)$ and $T_x(A')$ do not intersect for every pair of distinct cells $A$ and $A'$ of $\chi$, then $T_x$ displays $\chi$. A perfect phylogeny for a set of partial characters $\mathcal{C}$ is an $X$–tree $T_x$ that displays each character in $\mathcal{C}$. When $\mathcal{C}$ has a perfect phylogeny, we also say that $\mathcal{C}$ is compatible. The perfect phylogeny problem (also called the character compatibility problem) is to determine if a set of partial characters is compatible.
The perfect phylogeny problem reduces to a graph theoretical problem that we detail now. Given a set of characters \( C \), one can construct the partition intersection graph \( \text{int}(C) \) as follows. The vertex set of \( \text{int}(C) \) is 
\[ \{(A, \chi) \mid \chi \in C \text{ and } A \text{ is a cell of } \chi\} , \]
and there is an edge between two vertices \((A, \chi)\) and \((A', \chi')\) if and only if \( A \) and \( A' \) have non-empty intersection. For a vertex \((A, \chi)\) of \( \text{int}(C) \), \( A \) is the cell of \((A, \chi)\) and \( \chi \) is the character of \((A, \chi)\). Observe that if \( \chi = A_1 | A_2 | ... | A_r \) is a partial character, then every pair of distinct vertices \((A, \chi)\) and \((A', \chi)\) are non-adjacent in \( \text{int}(C) \).

A graph is chordal if every cycle of length four or more has a chord, that is, an edge between vertices of the cycle that do not appear consecutively in the cycle. In general \( \text{int}(C) \) is not a chordal graph, and we are interested in adding edges to \( \text{int}(C) \) to obtain a chordal supergraph \( H \) of \( \text{int}(C) \) that is called a triangulation of \( \text{int}(C) \). The added edges are called fill edges. If no subset of the fill edges yields a triangulation of \( \text{int}(C) \), it is a minimal triangulation of \( \text{int}(C) \). When each fill edge is of the form \((A, \chi)(A', \chi')\) and \( \chi \neq \chi' \), the resulting triangulation is a proper triangulation of \( \text{int}(C) \). The following classic result reduces the question of determining compatibility to finding proper triangulations of the partition intersection graph. It was originally phrased in terms of proper triangulations, but from the definitions it follows that \( \text{int}(C) \) has a proper triangulation if and only if it has a proper minimal triangulation.

**Theorem 1.** \([6, 21, 26]\) Let \( C \) be a set of qualitative characters. Then \( C \) is compatible if and only if \( \text{int}(C) \) has a proper minimal triangulation.

Two \( X \)–trees \( T_x \) and \( T'_x \) are isomorphic, writing \( T_x \cong T'_x \), if there is a bijective map \( \psi : V(T) \rightarrow V(T') \) that has the following properties:
1. it preserves labels, meaning that $\phi' = \psi \circ \phi$; and
2. it is a graph isomorphism, that is, $uv \in E(T)$ if and only if $\psi(u)\psi(v) \in E(T')$.

A set of characters $\mathcal{C}$ defines a perfect phylogeny if it is the unique perfect phylogeny, up to isomorphism, for $\mathcal{C}$. The unique perfect phylogeny problem is to determine if a set $\mathcal{C}$ of partial characters defines a perfect phylogeny. If $\mathcal{T}_x = (T, \phi)$ displays $\chi$ and $uv$ is an edge of $T$ such that $u$ is a node of $\mathcal{T}_x(A)$ and $v$ is a node of $\mathcal{T}_x(A')$ where $A$ and $A'$ are distinct cells of $\chi$, then $uv$ is distinguished by $\chi$. If every edge of $\mathcal{T}_x$ is distinguished by at least one character of $\mathcal{C}$, then $\mathcal{T}_x$ is distinguished by $\mathcal{C}$. The following characterization is due to Semple and Steel.

**Theorem 2.** [24] Let $\mathcal{C}$ be a set of partial characters on $X$. Then $\mathcal{C}$ defines a perfect phylogeny if and only if the following conditions are satisfied:

(a) $\operatorname{int}(\mathcal{C})$ has a unique proper minimal triangulation $H$; and
(b) there is a free ternary perfect phylogeny for $\mathcal{C}$ and it is distinguished by $\mathcal{C}$.

Further, if $\mathcal{T}_x$ is the unique perfect phylogeny for $\mathcal{C}$, then $\mathcal{T}_x$ is a free ternary $X$-tree distinguished by $\mathcal{C}$, and $\operatorname{int}(\mathcal{C}, \mathcal{T}_x) = H$.

This result is the impetus of our current work, and one of our main interests is to re-formulate condition (b) in terms of combinatorial structures that play a significant role in the study of chordal graphs and minimal triangulations.

Chordal graphs are characterized by the existence of trees that represent the adjacency structure of the graph. Suppose $G$ is a graph with vertices $V(G) = \{x_1, x_2, \ldots, x_n\}$. A tree representation of $G$ consists of a tree $T$ and subtrees $T_1, T_2, \ldots, T_n$ of $T$ such that two trees $T_i$ and $T_j$ intersect if and only if $x_i$ and $x_j$ are adjacent. Here, the subtrees are in one-to-one correspondence with the vertex set of $G$, and this correspondence is made explicit by mapping each subtree $T_i$ to the vertex $x_i$ of $G$. Observe that a node $v$ of $T$ defines a clique $\mathcal{K}(v) = \{x_i \mid v \text{ is a node of } T_i\}$ of $G$. Notationally, we will write a tree representation as an ordered pair $\mathcal{T}_r = (T, \mathcal{K})$ where $\mathcal{K}$ maps nodes of $T$ to cliques of $G$ satisfying the following properties:

(Edge Coverage) a pair of vertices $x$ and $y$ of $G$ are adjacent if and only if there is a node $v$ of $T$ such that $x, y \in \mathcal{K}(v)$; and

(Convexity) for each vertex $x$ of $G$, the set of nodes \( \{v \in V(T) \mid x \in \mathcal{K}(v)\} \)
induces a subtree of $T$ (i.e. a connected subgraph of $T$).

We will frequently refer to the convexity property throughout the paper. As with $X$-trees, we will call $T$ the underlying tree of $\mathcal{T}_r$. Often we will define a tree representation by only specifying the underlying tree $T$ and a collection of subtrees of $T$, which together implicitly define $\mathcal{K}$.

Let $T_1, T_2, \ldots, T_k$ be a collection of subtrees of $T$. If each pair $T_i, T_j$ of subtrees intersect at a node $v_{ij}$, then by the Helly property for subtrees of a tree [9], all of $T_1, T_2, \ldots, T_k$ intersect at a common node $v$. This property manifests itself as a statement about cliques of $G$ and nodes of $\mathcal{T}_r$ in the following way: for any clique $K$ of $G$, there is at least one node $u$ of $T$ such that $K \subseteq \mathcal{K}(u)$. In
particular, this is true when $K$ is a maximal clique of $G$ (i.e. no proper superset is also a clique), and therefore $K(V(T))$ contains the set of maximal cliques of $G$. If the maximal cliques of $G$ are in one-to-one correspondence with the nodes of $T$ via $K$, then $T_r$ is a clique tree of $G$. See Figure 2 for an example.

**Theorem 3.** [6, 8, 27] The following statements are equivalent.

(a) $G$ is a chordal graph.
(b) $G$ has a tree representation.
(c) $G$ has a clique tree.

Observe that if $T_r = (T, K)$ is a clique tree of $G$ and $uv$ is an edge of $T$, then because $K(u)$ and $K(v)$ are both maximal cliques of $G$, there is a vertex $x$ of $G$ in $K(u) - K(v)$. In general, a chordal graph has an exponential number of clique trees. An algorithm to enumerate clique trees, along with a formula to count them, appears in [16].

We will often be analyzing a tree representation $T_r = (T, K)$ of a triangulation $H$ of $\text{int}(C)$. Given a vertex $(A, \chi)$ of $\text{int}(C)$, we will denote the subtree of $T$ that it corresponds to by $T_r(A, \chi)$. Observe that $v$ is a node of $T_r(A, \chi)$ if and only if $(A, \chi) \in K(v)$. Given a set of characters $C$ on $X$ and an $X$–tree $T_x = (T, \phi)$, a chordal graph $\text{int}(C, T_x)$ is given by adding an edge between two vertices $(A_1, \chi_1)$ and $(A_2, \chi_2)$ if and only if $T_x(A_1)$ and $T_x(A_2)$ intersect. This construction, along with the fact that $\text{int}(C, T_x)$ is a triangulation of $\text{int}(C)$, is well-known in the phylogenetics literature, and will be discussed in detail in Section 2.

A chordal graph $G$ is uniquely representable if it has a single clique tree, or *ur-chordal* for short. A ur-chordal graph is ternary if each internal node of its clique tree has degree three, and its leafage is the number of leaves its clique tree has. Let $H$ be a proper triangulation of $\text{int}(C)$ and $T_r = (T, K)$ be a clique tree of $H$. An edge $uv$ of $T_r$ is incontractable with respect to $\chi$ if there are distinct cells $A$ and $A'$ of $\chi$ such that $u \in T_r(A, \chi)$ and $v \in T_r(A', \chi)$. We say that $T_r$ is incontractable with respect to $C$ if each edge is incontractable with respect to at least one $\chi \in C$. Now we present our first main result.

**Theorem 4.** Suppose $C$ is a set of partial characters on $X$. Then $C$ defines a perfect phylogeny if and only if the following conditions hold:

(a) $\text{int}(C)$ has a unique proper minimal triangulation $H$;
(b) $H$ is a ternary ur-chordal graph with leafage $|X|$; and
(c) each edge of $H$’s unique clique tree is incontractable with respect to $C$.

Further, if $T_x$ is the perfect phylogeny defined by $C$, then $T_x$ is a free ternary $X$–tree distinguished by $C$, and $\text{int}(C, T_x) = H$.

Let $C$ be a set of partial characters on $X$ and $\chi \in C$. Suppose $H$ is a triangulation of $\text{int}(C)$ with fill edge $(A, \chi)(A', \chi)$ where $A$ and $A'$ are distinct cells of $\chi$.

1 In general, the leafage of a chordal graph is the minimum number of leaves that a clique tree of the graph can have [19].
Then we say that \((A, \chi)(A', \chi)\) breaks \(\chi\), and \(\chi\) is a broken character of \(H\). For a triangulation \(H\) of \(\text{int}(C)\), its displayed characters are the characters of \(C\) that are not broken characters of \(H\). Bordewich, Huber, and Semple \(3\) proved that it is possible to find a maximum-sized compatible subset of \(C\) using the partition intersection graph.

**Theorem 5.** Let \(C\) be a set of partial characters on \(X\). Then \(C'\) is a maximum-sized compatible subset of \(C\) if and only if there is a triangulation \(H\) of \(\text{int}(C)\) that has \(C'\) as its displayed characters, and any other triangulation of \(\text{int}(C)\) has at most \(|C'|\) displayed characters.

A subset of partial characters \(C' \subseteq C\) is a maximal defining subset of \(C\) when \(C'\) defines a perfect phylogeny, and there is no compatible set \(C''\) such that \(C' \subset C'' \subset C\). Our second main result is the following.

**Theorem 6.** Suppose \(C\) is a set of partial characters on \(X\) and \(C' \subseteq C\). Then \(C'\) is a maximal defining subset of \(C\) if and only if the following conditions hold:

- (a) \(\text{int}(C)\) has a unique minimal triangulation \(H\) that has \(C'\) as its displayed characters, and no other minimal triangulation of \(\text{int}(C)\) has at least \(C'\) as its displayed character set;
- (b) \(H\) is a ternary ur-chordal graph with leafage \(|X|\); and
- (c) each edge of \(H\)'s unique clique tree is incontractable with respect to \(C'\).

Further, if \(T_x\) is the perfect phylogeny defined by \(C'\), then \(T_x\) is a free ternary \(X\)–tree distinguished by \(C'\), and \(\text{int}(C, T_x) = H\).

### 2 Chordal Graph Preliminaries

In this section, we detail known results on chordal graphs that are necessary for the remainder of the paper. Suppose \(G = (V, E)\) is a graph and \(S \subseteq V\). Let \(G - S\) denote the graph obtained from \(G\) by removing \(S\) and all edges incident to at least one vertex in \(S\). If there are vertices \(x\) and \(y\) of \(G\) that are connected in \(G\) but not in \(G - S\), then \(S\) is an \(xy\)–separator, and if no proper subset of \(S\) has this property, it is a minimal \(xy\)–separator. When \(S\) is a minimal \(xy\)–separator for at least one pair of vertices \(x\) and \(y\), it is a minimal separator. Minimality in this definition is relative; it is possible to have containment relationships between two minimal separators. The maximal connected subsets of \(G - S\) are the connected components of \(G - S\). Let \(C\) be a connected component of \(G - S\). The neighborhood of \(C\) in \(G\), denoted \(N(C)\), is the set of vertices of \(S\) that are adjacent to at least one vertex in \(C\). If \(N(C) = S\), then it is a full component of \(G - S\). The following useful characterization of minimal separators is well-known, and left as an exercise in \(9\).

 Dirac \(7\) called these sets relatively minimal cut-sets, which is perhaps more descriptive, but this term has stuck in the modern literature on chordal graphs and minimal triangulations.
Fig. 2. A chordal graph $G$ and clique tree $T_r = (T, K)$ of $G$. There are three clique trees for $G$, one of which is obtained by removing the bottom-leftmost node and its incident edge, and then attaching it to $v$. The maximal clique map $K$ is defined by the triangle drawn inside each node. Arrows indicate vertices that consist of the intersection of a neighboring node’s maximal clique, and each such intersection is a minimal separator by Theorem 7.

**Lemma 1.** Let $G = (V, E)$ be a graph, and $S \subseteq V$. Then $S$ is a minimal separator if and only if $G - S$ has two or more full components.

A minimal separator has *multiplicity* $k$ if $G - S$ has $k - 1$ full components. Interestingly, clique trees contain detailed information about the minimal separators of the graph it represents, which will be useful for our proofs in later sections.

**Theorem 7.** \cite{16, 20} Suppose $G = (V, E)$ is a chordal graph, $T_r = (T, K)$ is a clique tree of $G$, and $S \subseteq V$. Then $S$ is a minimal separator of $G$ if and only if there is an edge $uv$ of $T$ such that $S = K(u) \cap K(v)$. Further, the multiplicity of $S$ is the number of edges of $T$ with this property.

We will not need all of the following characterizations of ur-chordal graphs, but we list them for completeness.

**Theorem 8.** \cite{14, 18} Let $G$ be a chordal graph. Then the following statements are equivalent.

- **a)** $G$ is uniquely representable.
- **b)** If $S$ is a minimal separator of $G$, then there are exactly two maximal cliques $K$ and $K'$ of $G$ such that $S \subseteq K, K'$.
- **c)** Each minimal separator of $G$ has multiplicity one.

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3 This theorem also implies that a minimal separator of a chordal graph is a clique. In fact, chordal graphs are characterized by having only clique minimal separators, which is one of the earliest results on chordal graphs \cite{7}.
Lemma 2. There is no minimal separator of \( G \) that properly contains another minimal separator of \( G \).

Observation 1. Let \( C \) be a set of partial characters on \( X \), \( T_x \) be an \( X \)-tree, and \( T_r \) be the tree representation induced by \( T_x \). Then the underlying tree of \( T_r \) is the underlying tree of \( T_x \), and for all \( \chi \in C \) and cells \( A \) of \( \chi \), \( T_x(A) = T_r(A, \chi) \). Further, \( \text{int}(C, T_x) \) is a triangulation of \( \text{int}(C) \).

Lemma 2. Let \( C \) be a set of partial characters on \( X \), and \( T_x \) be an \( X \)-tree that displays \( C' \subseteq C \). Suppose that each edge of \( T_x \) is distinguished by \( C' \). Then the tree representation of \( \text{int}(C, T_x) \) derived from \( T_x \) is a clique tree of \( \text{int}(C, T_x) \).

Proof. Let \( T_r = (T, \mathcal{K}) \) be the tree representation of \( \text{int}(C, T_x) \) derived from \( T_x \). For the sake of contradiction, assume that \( T_r \) is not a clique tree, so that \( \mathcal{K} \) is not a one-to-one map between the nodes of \( T \) and the maximal cliques of \( \text{int}(C, T_x) \). Then there must be nodes \( u \) and \( v \) of \( T \) such that \( \mathcal{K}(v) \subseteq \mathcal{K}(u) \). Let \( v' \) be the
Without loss of generality, assume that the path from $u$ to $v$ intersect precisely when the corresponding vertices of $\text{int}(C, T_x)$ are adjacent. Observe that $T_x$ is not a clique tree; for example, the two left-most nodes map to non-maximal cliques. Additionally, there are two nodes that map to the maximal clique $\{cd, \chi_1\}, \{bde, \chi_2\}, \{de, \chi_3\}$. Obtaining a clique tree from a tree representation is described in [8].

Lemma 3. Let $C$ be a set of partial characters on $X$ and $T_x$ be an $X$–tree that displays $C' \subseteq C$. Suppose that $T_x$ is free, ternary, and each edge of $T_x$ is distinguished by $C'$. Then $\text{int}(C, T_x)$ is uniquely representable.

Proof. To prove that $\text{int}(C, T_x)$ is uniquely representable, we use Theorem [8] and show that there are no containment relationships between the minimal separators of $\text{int}(C, T_x)$. Working towards a contradiction, assume that $S \subset S'$ are minimal separators of $\text{int}(C, T_x)$, and let $T_x = (T, K)$ be the tree representation derived from $T_x$. Then $T_x$ is a clique tree by Lemma [2] and there are edges $w$ and $u'v'$ of $T$ such that $S = \mathcal{K}(u) \cap \mathcal{K}(v)$ and $S' = \mathcal{K}(u') \cap \mathcal{K}(v')$ by Theorem [7]. Without loss of generality, assume that the path from $v$ to $v'$ does not contain either $u$ or $u'$ (perhaps $v = v'$). Let $w$ be the node on this path adjacent to $v$ if $v \neq v'$, otherwise let $w = u'$. In either case, $\mathcal{K}(w)$ contains $S$: if $w = u'$, then $S \subseteq \mathcal{K}(w)$. Otherwise, each $(A, \chi)$ in $S$ is an element of both $\mathcal{K}(u)$ and $\mathcal{K}(u')$, so $(A, \chi) \in \mathcal{K}(w)$ by convexity, and $S \subseteq \mathcal{K}(w)$.

To complete the proof, we will obtain a contradiction by showing that $S$ has a vertex not in $\mathcal{K}(w)$. There is a character $\chi'$ in $C'$ that distinguishes $uv$, and distinct cells $A'$ and $A''$ of $\chi'$ such that $v$ is a node of $T_x(A')$ and $w$ is a closest node to $v$ between $u$ and $v$ in $T$, allowing the possibility that $v' = u$. Note that each vertex in $\mathcal{K}(v)$ is also a vertex of $\mathcal{K}(v')$ by convexity, so $\mathcal{K}(v) \subseteq \mathcal{K}(v')$.

Now, $vv'$ is distinguished by some $\chi \in C'$, so there are distinct cells $A$ and $A'$ of $\chi$ such that $v$ is a node of $T_x(A)$ and $v'$ is a node of $T_x(A')$. By Observation [4] v is a node of $T_x(A, \chi)$, so $(A, \chi) \in \mathcal{K}(v)$ and by containment $(A, \chi) \in \mathcal{K}(v')$. Further, $(A', \chi) \in \mathcal{K}(v')$, so $(A, \chi)(A', \chi)$ is a fill edge of $\text{int}(C, T_x)$ and it breaks $\chi$. This contradicts the assumption that $T_x$ displays $C'$, so $T_x$ must be a clique tree of $\text{int}(C, T_x)$. \hfill \Box

Fig. 3. The tree representation $T_r$ of $\text{int}(C, T_x)$ derived from $T_x$ in Figure 1.a. The triangulation $\text{int}(C, T_x)$ of $\text{int}(C)$ is depicted in Figure 1b; note that any two subtrees of $T_r$ intersect precisely when the corresponding vertices of $\text{int}(C, T_x)$ are adjacent.
node of $T_x(A')$. Now, $v$ has at least two neighbors, and because $T_x$ is ternary, $v$ must have degree three. Also, $v$ is not mapped to by $\phi$ because $T_x$ is free, so in order for $v$ to be a node of $T_x(A')$, there must be at least two nodes of $T_x$ in $\phi(A')$ that are not $v$, and the path between these two nodes must contain $v$. This path must also contain two of $v$’s neighbors, and neither of these vertices can be $w$, because $w$ is not a node of $T_x(A')$. Thus $u$ must be on this path, so it is a node of $T_x(A')$. Both $K(u)$ and $K(v)$ contain $(A', \chi')$ by Observation 4, so it must be a vertex of $S = K(u) \cap K(v)$. Further, $(A', \chi') \notin K(w)$ because $w$ is not a node of $T_x(A') = T_x(A', \chi')$. This is impossible because we have shown that both $(A', \chi') \in S - K(w)$ and $S \subseteq K(w)$. Thus there are no containment relationships between the minimal separators of int$(C, T_x)$, and int$(C, T_x)$ is uniquely representable by Theorem 8.

\[\square\]

Lemma 4. \[3\] Let $C$ be a set of partial characters on $X$, $T_x$ an $X$–tree, and $C'$ be the subset of $C$ displayed by $T_x$. Then int$(C, T_x)$ is a triangulation of int$(C)$ in which the displayed characters are $C'$.

The previous three lemmas can be summarized as follows.

Theorem 9. Let $C$ be a set of partial characters on $X$ and $T_x$ be an $X$–tree that displays $C' \subseteq C$. Suppose that $T_x$ is free, ternary, and each edge of $T_x$ is distinguished by $C'$. Then int$(C, T_x)$ is a uniquely representable chordal graph, and the tree representation derived from $T_x$ is its unique clique tree. Further, the displayed characters of int$(C, T_x)$ are exactly $C'$.

Now suppose that $T_x = (T, K)$ is a clique tree of a triangulation $H$ of int$(C)$, with the goal of defining an $X$–tree $T_x$. The discussion we provide here is standard, e.g. see \[3, 25\]. Construct a map $\phi$ from $X$ to $T$ by defining, for each $a \in X$, $\phi(a) = v$ if and only if $K(v)$ contains every vertex of int$(C)$ whose cell contains $a$. These vertices form a clique because $a$ is contained in each of their cells. Because we have only added fill edges to obtain $H$, this clique a subset of a maximal clique of $H$, and hence $v$ exists. There may be more than one choice for $v$, each of which we call a candidate node for $a$. Let $u$ be a leaf of $T$ with neighbor $w$. Then $K(u)$ is a maximal clique that contains a vertex $(A, \chi)$ of int$(C)$ that is not found in $K(w)$. By convexity, $u$ is the only node of $T$ whose corresponding maximal clique contains $(A, \chi)$. Each $a' \in A$ has $u$ as its unique candidate node, and hence every leaf of $T$ is a unique candidate node for at least one element of $X$. Thus each leaf of $T$ must be labeled by $\phi$. To finish constructing an $X$–tree, obtain $T'$ by suppressing any unlabeled nodes of $T$ that have degree two. The result is an $X$–tree $T_x = (T', \phi)$, and we say that $T_x$ induces $T_x$ and $T_x$ is induced by $T_x$. We emphasize that the underlying tree of $T_x$ need not be the same as the underlying tree of $T_x$. Note that, because an element of $X$ may have multiple candidate nodes, $T_x$ may induce multiple $X$–trees. Next, we show that when $H$ is a minimal triangulation, much of $T_x$‘s structure is described by $T_x$. The following lemma will be useful.

Lemma 5. \[17, 22\] Let $G$ be a graph and $H$ be a minimal triangulation of $G$. If $uv$ is a fill edge of $H$, then there is a minimal separator of $H$ that contains both $u$ and $v$. 

9
Fig. 4. A clique tree $\mathcal{T}'_r$ of $\text{int}(\mathcal{C}, \mathcal{T}_x)$ from Figure 1.b and an $X$–tree $\mathcal{T}'_x$ induced by $\mathcal{T}'_r$. Note that $\text{int}(\mathcal{C}, \mathcal{T}'_x) = \text{int}(\mathcal{C}, \mathcal{T}_x)$, where $\mathcal{T}_x$ is the $X$–tree from Fig. 1.a.

Though not stated in this form, the following lemma follows from the proof of Lemma 2.4 and the statement of Corollary 2.5 in [24].

**Lemma 6.** Let $H$ be a minimal triangulation of $\text{int}(\mathcal{C})$, and suppose $\mathcal{T}_x$ is induced by a clique tree of $H$. Then $H = \text{int}(\mathcal{C}, \mathcal{T}_x)$.

**Lemma 7.** Let $H$ be a minimal triangulation of $\text{int}(\mathcal{C})$, $\mathcal{T}_r = (T, \mathcal{K})$ be a clique tree of $H$, and suppose $\mathcal{T}_r$ induces $\mathcal{T}_x$. Then the underlying tree of $\mathcal{T}_x$ is $T$.

**Proof.** We have already seen that every leaf of $T$ is the unique candidate node of some element of $X$. In addition to this, it was also shown in [13] that if $u$ is a node of $\mathcal{T}_r$ of degree two, then $u$ is the unique candidate node of some element of $X$. This was done by showing that $\mathcal{K}(u)$ contains either:

1. a vertex $(A_1, \chi_1)$ of $\text{int}(\mathcal{C})$ that is not contained in $\mathcal{K}(w)$ for any other node $w \neq u$ of $T$; or
2. an edge $(A_2, \chi_2)(A_3, \chi_3)$ of $\text{int}(\mathcal{C})$, whose incident vertices have cells with non-empty intersection, and are not both contained in $\mathcal{K}(w)$ for any other node $w \neq u$ of $T$.

For completeness, we outline a proof here. Using convexity and the fact that $u$ has degree two, it follows that either a unique vertex or unique pair of vertices are contained in $\mathcal{K}(u)$. It remains to show that $(A_2, \chi_2)(A_3, \chi_3)$ is actually an edge of $\text{int}(\mathcal{C})$ (so $A_2 \cap A_3$ is non-empty). If not, then by Lemma 5 there is a minimal separator $S$ of $H$ containing both $(A_2, \chi_2)$ and $(A_3, \chi_3)$. By Theorem 7 there is an edge $u_1u_2$ of $T$ such that $S = \mathcal{K}(u_1) \cap \mathcal{K}(u_2)$. But this contradicts case 2, so it must be that $(A_2, \chi_2)(A_3, \chi_3)$ is an edge of $\text{int}(\mathcal{C})$.

In both cases, $u$ is the unique candidate node of some element in $X$ (this element is either $a \in A_1$ or $a \in A_2 \cap A_3$), so every degree two node of $T$ is labeled by $\phi$, and there are no nodes of $T$ that need to be suppressed. Hence the underlying tree of $\mathcal{T}_x$ is $T$. 

\[ \square \]
Lemma 8. Let $H$ be a minimal triangulation of $\text{int}(C)$, $T_r = (T,K)$ be a clique tree of $H$, and suppose $T_r$ induces $T_r$. Then for each vertex $(A,\chi)$ of $\text{int}(C)$, $T_\Delta(A) = T_r(A,\chi)$.

Proof. Let $(A,\chi)$ be a vertex of $\text{int}(C)$ and consider a node $v$ of $T_\Delta(A)$. Either $v = \phi(a)$ for some $a \in A$ or $v$ lies between $\phi(a_1)$ and $\phi(a_2)$ for some $a_1, a_2 \in A$. In the first case, $(A,\chi) \in K(v)$ because $v$ is a candidate node for $a$. Similarly, in the second case, $(A,\chi)$ is an element of both $K(\phi(a_1))$ and $K(\phi(a_2))$, and therefore $(A,\chi) \in K(v)$ by convexity. In both cases $v$ is a node of $T_r(A,\chi)$, so $T_\Delta(A) \subseteq T_r(A,\chi)$.

To finish proving equality, suppose that $T_\Delta(A) \subset T_r(A,\chi)$. Define a tree representation $T' = (T',K')$ of a graph $H'$ as follows: set $T' = T$, and define subtrees $T'_r(A',\chi')$ of $T$ for each vertex $(A',\chi')$ of $\text{int}(C)$ as follows:

1. $T'_r(A',\chi') = T_r(A',\chi')$ if $(A',\chi') \neq (A,\chi)$, and
2. $T'_r(A',\chi') = T_\Delta(A)$ if $(A',\chi') = (A,\chi)$.

We have already seen that $T'_r(A',\chi') \subseteq T_r(A',\chi')$ for every vertex $(A',\chi')$ of $\text{int}(C)$, so the edge set of $H'$ is a subset of the edge set of $H$. If $(A_1,\chi_1)(A_2,\chi_2)$ is an edge of $\text{int}(C)$, then $A_1$ and $A_2$ have at least one element $a$ in common, and thus $T_\Delta(A_1)$ and $T_\Delta(A_2)$ intersect at $\phi(a)$. Further, $T_\Delta(A') \subseteq T'_r(A',\chi')$ for each vertex $(A',\chi')$ of $\text{int}(C)$, so $T'_r(A_1,\chi_1)$ and $T'_r(A_2,\chi_2)$ also intersect at $\phi(a)$. Therefore $(A_1,\chi_1)(A_2,\chi_2)$ is an edge of $H'$, and $H'$ is chordal by Theorem 3 so it is a triangulation of $\text{int}(C)$.

To complete the proof, we show that $H'$ must have an edge that does not exist in $H$. Because $T_\Delta(A) \subset T_r(A,\chi)$, there is a node $u$ of $T_r(A,\chi) - T_\Delta(A)$ that is adjacent to a node $w$ of $T_\Delta(A) = T_r(A,\chi)$. By maximality, there is a vertex $(A',\chi') \subseteq K(u) - K(w)$, and because $u$ is a node of $T_r(A,\chi)$, $(A,\chi) \in K(u)$. Therefore $(A',\chi')(A,\chi)$ is an edge of $H$. The situation in $H'$ is different: if $(A',\chi')(A,\chi)$ is an edge of $H'$, then $T'_r(A,\chi)$ and $T'_r(A',\chi')$ intersect at a node $v'$. But if $v'$ is a node of $T'_r(A,\chi)$, then $v'$ is on the path from $v'$ to $u$, and by convexity this would imply that $(A',\chi') \subseteq K(w)$. Hence $(A',\chi')(A,\chi)$ is not an edge of $H'$, so the edge set of $H'$ is a proper subset of the edge set of $H$. This is impossible because $H$ is a minimal triangulation of $\text{int}(C)$, so it must be that $T_\Delta(A) = T_r(A,\chi)$ for each vertex $(A,\chi)$ of $\text{int}(C)$.

Lemma 6, 7, and 8 are summarized below.

Theorem 10. Let $H$ be a minimal triangulation of $\text{int}(C)$, $T_r$ be a clique tree of $H$, and suppose $T_r$ induces $T_r$. Then the underlying tree of $T_\Delta$ is the underlying tree of $T_r$, and for each vertex $(A,\chi)$ of $\text{int}(C)$, $T_\Delta(A) = T_r(A,\chi)$. Further, $H = \text{int}(C,T_\Delta)$.

4 Maximal Defining Subsets of Characters

This section is devoted to the proof of Theorem 6. Its proof will follow mainly from Propositions 1 and 2. Recall that, for a graph $H$ and a subset $U$ of its
vertices, the graph $H - U$ is obtained by removing the vertices in $U$ and edges of $H$ incident to one or more vertices of $U$.

**Lemma 9.** Let $C$ be a set of partial characters and $C' \subseteq C$. Suppose $H'$ is a minimal triangulation of $\text{int}(C')$, and let $U$ be the vertices of $\text{int}(C)$ that are not vertices of $\text{int}(C')$. Then there is a minimal triangulation $H$ of $\text{int}(C)$ such that $H' = H - U$.

**Proof.** Let $H'$ be a minimal triangulation of $\text{int}(C')$ and $H^*$ be the graph obtained by adding the following fill edges to $\text{int}(C)$:

1. the fill edges of $H'$; and
2. fill edges of the form $(A, \chi)(A', \chi')$ where $(A, \chi)$ is a vertex of $U$, and $(A', \chi')$ is any vertex of $\text{int}(C)$.

First we prove that $H^*$ is chordal, and then we will use it to construct $H$, a minimal triangulation of $\text{int}(C)$ such that $H - U = H'$.

Let $(A_1, \chi_1), (A_2, \chi_2), \ldots, (A_k, \chi_k)$ be a cycle in $H^*$. If $\chi_i \in C'$ for all $i = 1, 2, \ldots, k$, then this cycle is also a cycle of $H'$, and therefore has a chord that is an edge of $H'$. Each edge of $H'$ is also an edge of $H^*$, so this cycle has a chord in $H^*$. Otherwise, without loss of generality, $\chi_1 \in C - C'$ and $(A_1, \chi_1) \in U$ so either $(A_1, \chi_1)(A_3, \chi_3)$ is an edge of $\text{int}(C)$ or is a fill edge of $H^*$ of type 2. In either case, this cycle has a chord, so $H^*$ is chordal.

Now let $H$ be any minimal triangulation of $\text{int}(C)$ such that the edge set of $H$ is a subset of the edge set of $H^*$. Every edge of $H - U$ is either an edge of $\text{int}(C')$ or is an edge of $H'$ by the construction of $H^*$ and $H$. Therefore the edge set of $H - U$ is a subset of the edge set of $H'$. Further, $H - U$ is chordal because any cycle of $H - U$ is a cycle of $H$ (i.e. chordality is inherited), so it is a triangulation of $\text{int}(C')$. By minimality of $H'$, it must be that the edge set of $H - U$ is equal to the edge set of $H'$, so $H' = H - U$. \qed

**Lemma 10.** [12] see also [3] Let $C$ be a set of partial characters on $X$ and suppose that $C'$ is a compatible subset of $C$. Then there is a minimal triangulation of $\text{int}(C)$ whose displayed characters are at least $C'$.

Though not stated in this form, the following lemma is a direct result of Lemma 5.1 in [3] and its proof.

**Lemma 11.** Let $C$ be a set of partial characters on $X$. Suppose $H$ is a triangulation of $\text{int}(C)$ with displayed characters $C'$. Then if $T_x$ is induced by a clique tree of $H$, it is a perfect phylogeny for $C'$.

**Proposition 1.** Let $C$ be a set of partial characters on $X$ and $C' \subseteq C$. Suppose that the following conditions hold:

(i) $\text{int}(C)$ has a unique minimal triangulation $H$ that has $C'$ as its displayed characters, and no other minimal triangulation of $\text{int}(C)$ has at least $C'$ as its displayed character set;

(ii) $H$ is a ternary ur-chordal graph with leafage $|X|$; and
(iii) each edge of $H$’s unique clique tree is incontractable with respect to $C'$.

Then $C'$ is a maximal defining subset of $C$.

Proof. We begin by showing that $C'$ has a unique perfect phylogeny using Theorem 2 and finish the proof showing that no superset of $C'$ has a unique perfect phylogeny.

Throughout the proof, $H$ will denote the unique minimal triangulation of $\text{int}(C)$ given by (i) whose displayed character set is $C'$. By Lemma 11 $C'$ has a perfect phylogeny so it is compatible. There is a proper triangulation of $\text{int}(C')$ by Theorem 1, so $\text{int}(C')$ has a proper minimal triangulation as well. To see that condition (a) of Theorem 2 holds, suppose that $H_1'$ and $H_2'$ are proper minimal triangulations of $\text{int}(C')$ given by Theorem 1 and let $U$ be the set of vertices of $\text{int}(C)$ not in $\text{int}(C')$. By Lemma 9 there are minimal triangulations $H_1$ and $H_2$ of $\text{int}(C)$ that satisfy $H_1' = H_1 - U$ and $H_2' = H_2 - U$. The displayed characters of $H_1$ and $H_2$ must be at least $C'$, because any fill edge that breaks a character of $C'$ would also appear in $H_1'$ or $H_2'$, and both $H_1'$ and $H_2'$ are proper triangulations of $\text{int}(C')$. By (i), we have $H_1 = H = H_2$. Therefore $H_1' = H - U = H_2'$, so condition (a) of Theorem 2 is satisfied with respect to $C'$.

Now we show condition (b) of Theorem 2 holds. Let $T_r$ be the unique clique tree of $H$ given by (ii), and suppose $T_x$ is the $X$-tree induced by $T_r$. $T_x$ displays $C'$ by Lemma 11 and by Theorem 10 the underlying tree of $T_x$ is also the underlying tree of $T_r$. Further, $T$ is ternary and has $|X|$ leaves by (ii), so $T_x$ must be free and ternary. To see that $T_x$ is distinguished by $C'$, consider an edge $uv$ of $T$. By (iii) $uv$ is incontractible with respect to $C'$, so there is a character $\chi \in C'$ and distinct cells $A$ and $A'$ of $\chi$ such that $u$ is a node of $T_r(A, \chi)$ and $v$ is a node of $T_r(A', \chi)$. But $T_x(A) = T_r(A, \chi)$ and $T_x(A') = T_r(A', \chi)$ by Theorem 10. Hence condition (b) of Theorem 2 also holds with respect to $C'$, so $C'$ defines $T_x$.

Last, we show that no proper superset of $C'$ also defines an $X$-tree. If any superset $C^*$ of $C'$ was compatible, then by Lemma 10 some minimal triangulation of $\text{int}(C)$ has at least $C^*$ as its displayed character set. This would contradict (i), so no such superset can exist. This completes the proof. □

Lemma 12. Suppose $C'$ is a maximal defining subset of $C$, and $H$, $H'$ are minimal triangulations of $\text{int}(C)$ with $C'$ as its displayed character set. Then $H = H'$.

Proof. Let $T_x$ be an $X$-tree induced by a clique tree $T_r$ of $H$ and $T'_x$ be an $X$-tree induced by a clique tree $T'_r$ of $H'$. By Lemma 11 $T_r$ and $T'_r$ are perfect phylogenies for $C'$, and because $C'$ defines an $X$-tree it must be that $T_x \cong T'_x$ via isomorphism $\psi$. Additionally, for each vertex $(A, \chi)$ of $\text{int}(C)$ we have $T_r(A, \chi) = T_x(A)$ and $T'_r(A, \chi) = T'_x(A)$ by Theorem 10.

To prove that $H = H'$, it suffices to show that their fill edge sets are the same. Suppose that $(A_1, \chi_1)(A_2, \chi_2)$ is a fill edge of $H$. By the edge coverage property of clique trees, $T_r(A_1, \chi_1)$ and $T_r(A_2, \chi_2)$ intersect at a node $v$ of $T$. We will show that $T'_r(A_1, \chi_1)$ and $T'_r(A_2, \chi_2)$ intersect at $\psi(v)$. If there is an $a \in A_1$ such that $\phi(a) = v$, then $\psi(v) = \phi'(a)$ is a node of $T'_x(A_1) = T'_r(A_1, \chi_1)$. Otherwise
there are $a_1, a_2 \in A_1$ and $v$ is an internal node on the path from $\phi(a_1) = v_1$
 to $\phi(a_2) = v_2$. Because $\psi$ is a graph isomorphism, $\psi(v)$ is an internal node on
 the path from $\psi(v_1)$ to $\psi(v_2)$. Further, $\psi(v_1)$ and $\psi(v_2)$ are nodes of $\mathcal{T}'_2(A_1) = \mathcal{T}'_2(A_1, \chi_1)$, so $\psi(v)$ is a node of $\mathcal{T}'_2(A_1, \chi_1)$ as well. In both cases $\psi(v)$ is a node of $\mathcal{T}'_2(A_1, \chi_1)$, and a similar argument shows that $\psi(v)$ is a node of $\mathcal{T}'_2(A_2, \chi_2)$. Therefore $\mathcal{T}'_2(A_1, \chi_1)$ and $\mathcal{T}'_2(A_2, \chi_2)$ intersect at $\psi(v)$, so $(A_1, \chi_1)(A_2, \chi_2)$ is a
 fill edge of $H'$, and the fill edge set of $H$ is a subset of the fill edge set of $H'$. A
 symmetric argument shows that the fill edge set of $H$ is a subset of the fill edge
 set of $H'$, so these fill edge sets must be equal, completing the proof. \qed

**Proposition 2.** Let $C$ be a set of partial characters on $X$ and $C'$ be a maximal
 defining subset of $C$. Then the following conditions hold:

(i) $\text{int}(C)$ has a unique minimal triangulation $H$ that has $C'$ as its displayed
 characters, and no other minimal triangulation of $\text{int}(C)$ has at least $C'$ as
 its displayed character set;

(ii) $H$ is a ternary ur-chordal graph with leafage $|X|$; and

(iii) each edge of $H$’s unique clique tree is incontractable with respect to $C'$.

Further, if $C'$ defines $\mathcal{T}_x$, then $\text{int}(C, \mathcal{T}_x) = H$.

**Proof.** To see that (i) holds, first observe that $C'$ is compatible by definition.
There is a minimal triangulation $H_1$ of $\text{int}(C)$ with at least $C'$ as its displayed
 character set by Lemma 10. Because $C'$ is a maximal defining subset of $C$, there
 is no $C' \subset C' \subseteq C$ that is compatible. By Lemma 11, the displayed characters of
 $H_1$ are compatible, so this set must be exactly $C'$. This is true of any minimal triangulation of $\text{int}(C)$ that has at least $C'$ as its displayed characters. If $H_2$ is
 such a minimal triangulation, then $H_1 = H_2$ by Lemma 12 so there is a unique
 minimal triangulation of $\text{int}(C)$ that has at least $C'$ as its displayed characters.
 We will refer to this unique minimal triangulation as $H$ in the remainder of the
 proof.

Now we show that (ii) holds. Let $\mathcal{T}_x$ be the $X$–tree induced by a clique tree
 of $H$. By Lemma 11, $\mathcal{T}_x$ is a perfect phylogeny for $C'$, and since $C'$ is a maximal
 defining subset it must be that $C'$ defines $\mathcal{T}_x$. Recall that $\mathcal{T}_x$ is free, ternary, and distinguished by $C'$ according to Theorem 2. By Theorem 9, $\text{int}(C, \mathcal{T}_x)$ is ur-
 chordal. On the other hand, $H = \text{int}(C, \mathcal{T}_x)$ by Theorem 10 so $H$ is ur-chordal
 as well. By the same theorem, $H$’s unique clique tree has the same underlying
tree as $\mathcal{T}_x$. Since $\mathcal{T}_x$ is ternary, this clique tree must also be ternary, so $H$ is a
 ternary ur-chordal graph. This proves statement (ii).

Now consider condition (iii), and let $uv$ be an edge of $T$. By Theorem 2, the edge $uv$
 is distinguished by $C'$, so there is a character $\chi \in C'$ that has cells
 $A \neq A'$ and $u$ is a node of $\mathcal{T}_x(A)$ and $v$ is a node of $\mathcal{T}_x(A')$. From Theorem 10 we
 see that $\mathcal{T}_x(A) = \mathcal{T}_x(A, \chi)$ and $\mathcal{T}_x(A') = \mathcal{T}_x(A', \chi)$, so $uv$ is incontractable with
 respect to $C'$. Hence $\mathcal{T}_x$ is incontractable with respect to $C'$.

The remainder of the theorem was shown while proving (ii) holds. \qed

**Proof of Theorem 6.** Propositions 1 and 2 show that $C'$ is a maximal defining
 subset of $C$ if and only if conditions (a) – (c) hold. The fact that $\mathcal{T}_x$ is free,
ternary, and distinguished by $C'$ follows by Theorem 2. Finally, $\text{int}(C, T_x) = H$ due to Proposition 2.

$\square$

**Proof of Theorem 4.** Use Theorem 6 taking $C' = C$. $\square$

## 5 Discussion

We conclude with a brief discussion on the role minimal separators play in minimal triangulation theory [15], and how our characterization may contribute towards constructing an algorithm that sometimes finds a maximal defining subset of characters when one exists. Minimal triangulations have been characterized by their minimal separators, which happen to be minimal separators of the triangulated graph as well [17, 22]. Further, a minimal separator of a minimal triangulation has connected components (and full components) that are identical in the graph that has been triangulated [15].

Bouchitté and Todinca [4, 5] used minimal separators and potential maximal cliques, the maximal cliques of minimal triangulations, to create a dynamic programming algorithm to solve the treewidth and minimum-fill problems in time polynomial in the number of minimal separators of a graph. This approach was extended to create a dynamic programming algorithm that solves a variety perfect phylogeny problems in [11], including the unique perfect phylogeny problem.

Our results elucidate the structure of minimal separators of triangulations associated with maximal defining subsets of characters. This structure is retained in the partition intersection graph, and is closely related to the structure of potential maximal cliques, because the connected components obtained by removing the vertices in a potential maximal clique have neighborhoods that are minimal separators [4]. This may allow for the computation of a ternary ur-chordal minimal triangulation in time polynomial in the number of minimal separators of $\text{int}(C)$ (or asserting that no ternary ur-chordal minimal triangulations exist), yielding a candidate subset $C'$ of $C$ that may be a maximal subset of characters. The number of minimal separators of $\text{int}(C')$ is bounded by the number of minimal separators of $\text{int}(C)$ (this is a specific example of a more general fact; see Corollary 4 in [5]). Therefore if it is computationally feasible to find $C'$ due to $\text{int}(C)$ having a small number of minimal separators, checking if $C'$ defines a perfect phylogeny using the method from [11] may also be feasible.

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References

1. Anne Berry and Romain Pogorelcnik. A simple algorithm to generate the minimal separators and the maximal cliques of a chordal graph. *Information Processing Letters*, 111(11):508–511, 2011.
2. J.R.S. Blair and B.W. Peyton. An introduction to chordal graphs and clique trees. In J.A. George, J.R. Gilbert, and J.W-H. Liu, editors, *Graph Theory and Sparse Matrix Computations*, volume 56 of *IMA Volumes in Mathematics and its Applications*, pages 1–27. Springer–Verlag.
3. M. Bordewich, K.T. Huber, and C. Semple. Identifying phylogenetic trees. *Discrete Mathematics*, 300(1–3):30–43, 2005.
4. V. Bouchitté and I. Todinca. Treewidth and minimum fill-in: grouping the minimal separators. *SIAM Journal on Computing*, 31(1):212–232, 2001.
5. V. Bouchitté and I. Todinca. Listing all potential maximal cliques of a graph. *Theoretical Computer Science*, 276(1-2):17–32, 2002.
6. P. Buneman. A characterisation of rigid circuit graphs. *Discrete Mathematics*, 9(3):205–212, 1974.
7. G.A. Dirac. On rigid circuit graphs. *Abhandlungen aus dem Mathematischen Seminar der Universität Hamburg*, 25(1–2):71–76, 1961.
8. F. Gavril. The intersection graphs of subtrees in trees are exactly the chordal graphs. *Journal of Combinatorial Theory*, 16(1):47–56, 1974.
9. M.C. Golumbic. *Algorithmic graph theory and perfect graphs*. Elsevier Science, 2nd edition edition, 2004.
10. Dan Gusfield. The multi-state perfect phylogeny problem with missing and removable data: solutions via integer–programming and chordal graph theory. *Journal of Computational Biology*, 17(3):383–399, 2010.
11. R. Gysel. Potential maximal clique algorithms for perfect phylogeny problems. Pre-print: arXiv, 1303.3931.
12. R. Gysel and D. Gusfield. Extensions and improvements to the chordal graph approach to the multistate perfect phylogeny problem. *IEEE/ACM Transactions on Computational Biology and Bioinformatics*, 8(4):912–917, 2011.
13. R. Gysel, F. Lam, and D. Gusfield. Constructing perfect phylogenies and proper triangulations for three-state characters. *Algorithms for Molecular Biology*, 7:26, 2012.
14. H. Hara and A. Takemura. Boundary cliques, clique trees and perfect sequences of maximal cliques of a chordal graph. *Technical Report METR 2006-41, Department of Mathematical Informatics, University of Tokyo*, 2006.
15. P. Hegernes. Minimal triangulations of graphs: a survey. *Discrete Mathematics*, 306(3):297–317, 2006.
16. C. Ho and R.C.T. Lee. Counting clique trees and computing perfect elimination schemes in parallel. *Information Processing Letters*, 31(2):61–68, 1989.
17. T. Kloks, D. Kratsch, and J. Spinrad. On treewidth and minimum fill-in of asteroidal triple-free graphs. *Theoretical Computer Science*, 175(2):309–335, 1997.
18. P.S. Kumar and C.E.V. Madhavan. Clique tree generalization and new subclasses of chordal graphs. *Discrete Applied Mathematics*, 117(1–3):109–131, 2002.
19. I.J. Lin, T.A. McKee, and D.B. West. The leafage of a chordal graph. *Discussiones Mathematicae Graph Theory*, 18:23–48, 1998.
20. T.A. McKee and F.R. McMorris. *Topics in Intersection Graph Theory*, Number 2 in SIAM Monographs on Discrete Mathematics and Applications. 1999.
21. C.A. Meacham. Theoretical and computational considerations of the compatibility of qualitative taxonomic characters. In J. Felsenstein, editor, *Numerical Taxonomy*, volume 1 of *NATO ASI Series G*, pages 304–314. Springer–Verlag, 1983.
22. A. Parra and P. Scheffler. Characterizations and algorithmic applications of chordal graph embeddings. *Discrete Applied Mathematics*, 79(1–3):171–188, 1997.
23. D.J. Rose. Triangulated graphs and the elimination process. *Journal of Mathematical Analysis and Applications*, 32(3):597–609, 1970.
24. C. Semple and M. Steel. A characterization for a set of partial partitions to define an X-tree. *Discrete Mathematics*, 247(1–3):169–186, 2002.
25. C. Semple and M. Steel. *Phylogenetics*. Oxford Lecture Series in Mathematics and Its Applications. Oxford University Press, 2003.
26. M. Steel. The complexity of reconstructing trees from qualitative characters and subtrees. *Journal of Classification*, 9(1):91–116, 1992.
27. J.R. Walter. Representations of chordal graphs as subtrees of a tree. *Journal of Graph Theory*, 2(3):265–267, 1978.