

# Algorithms for the Majority Rule (+) Consensus Tree and the Frequency Difference Consensus Tree

Jesper Jansson<sup>1,\*</sup>, Chuanqi Shen<sup>2</sup>, and Wing-Kin Sung<sup>3,4</sup>

<sup>1</sup> Laboratory of Mathematical Bioinformatics (Akutsu Laboratory),  
Institute for Chemical Research,  
Kyoto University, Gokasho, Uji, Kyoto 611-0011, Japan  
jj@kuicr.kyoto-u.ac.jp

<sup>2</sup> Stanford University, 450 Serra Mall, Stanford, CA 94305-2004, USA  
shencq@stanford.edu

<sup>3</sup> School of Computing, National University of Singapore, 13 Computing Drive,  
Singapore 117417  
ksung@comp.nus.edu.sg

<sup>4</sup> Genome Institute of Singapore, 60 Biopolis Street, Genome, Singapore 138672

**Abstract.** This paper presents two new deterministic algorithms for constructing consensus trees. Given an input of  $k$  phylogenetic trees with identical leaf label sets and  $n$  leaves each, the first algorithm constructs the *majority rule (+) consensus tree* in  $O(kn)$  time, which is optimal since the input size is  $\Omega(kn)$ , and the second one constructs the *frequency difference consensus tree* in  $\min\{O(kn^2), O(kn(k + \log^2 n))\}$  time.

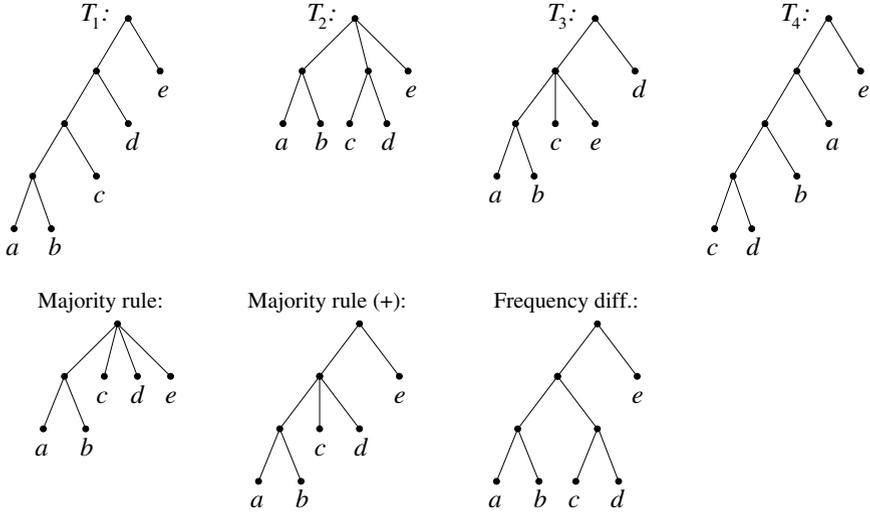
## 1 Introduction

A *consensus tree* is a phylogenetic tree that summarizes a given collection of phylogenetic trees having the same leaf labels but different branching structures. Consensus trees are used to resolve structural differences between two or more existing phylogenetic trees arising from conflicts in the raw data, to find strongly supported groupings, and to summarize large sets of candidate trees obtained by bootstrapping when trying to infer a new phylogenetic tree accurately [2, 10, 12, 27].

Since the first type of consensus tree was proposed by Adams III [1] in 1972, many others have been defined and analyzed. See, e.g., [5], Chapter 30 in [12], or Chapter 8.4 in [27] for some surveys. Which particular type of consensus tree to use in practice depends on the context. For example, the *strict consensus tree* [25] is very intuitive and easy to compute [9] and may be sufficient when there is not so much disagreement in the data, the *majority rule consensus tree* [21] is “the optimal tree to report if we view the cost of reporting an estimate of the phylogeny to be a linear function of the number of incorrect clades in the estimate and the number of true clades that are missing from the estimate and we

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\* Funded by The Hakubi Project and KAKENHI grant number 23700011.



**Fig. 1.** Let  $\mathcal{S} = \{T_1, T_2, T_3, T_4\}$  as shown above with  $L = \Lambda(T_1) = \Lambda(T_2) = \Lambda(T_3) = \Lambda(T_4) = \{a, b, c, d, e\}$ . The only non-trivial majority cluster of  $\mathcal{S}$  is  $\{a, b\}$ , the non-trivial majority (+) clusters of  $\mathcal{S}$  are  $\{a, b\}$  and  $\{a, b, c, d\}$ , and the non-trivial frequency difference clusters of  $\mathcal{S}$  are  $\{a, b\}$ ,  $\{a, b, c, d\}$ , and  $\{c, d\}$ . The majority rule, majority rule (+), and frequency difference consensus trees of  $\mathcal{S}$  are displayed.

view the reporting of an incorrect grouping as a more serious error than missing a clade” [16], and the  $R^*$  consensus tree [5] provides a statistically consistent estimator of the species tree topology when combining gene trees [10]. Therefore, scientists need efficient algorithms for constructing a broad range of different consensus trees.

In a recent series of papers [8, 17–19], we have developed fast algorithms for computing the *majority rule consensus tree* [21], the *loose consensus tree* [4] (also known in the literature as the *combinable component consensus tree* or the *semi-strict consensus tree*), a *greedy consensus tree* [5, 13], the  $R^*$  consensus tree [5], and consensus trees for so-called *multi-labeled phylogenetic trees (MUL-trees)* [20]. In this paper, we study two relatively new types of consensus trees called the *majority rule (+) consensus tree* [7, 11] and the *frequency difference consensus tree* [14], and give algorithms for constructing them efficiently.

## 1.1 Definitions and Notation

We shall use the following basic definitions. A *phylogenetic tree* is a rooted, unordered, leaf-labeled tree in which every internal node has at least two children and all leaves have different labels. (Below, phylogenetic trees are referred to as “trees” for short). For any tree  $T$ , the set of all nodes in  $T$  is denoted by  $V(T)$  and the set of all leaf labels in  $T$  by  $\Lambda(T)$ . Any nonempty subset  $C$  of  $\Lambda(T)$  is called a *cluster* of  $\Lambda(T)$ ; if  $|C| = 1$  or  $C = \Lambda(T)$  then  $C$  is *trivial*, and otherwise,

$C$  is *non-trivial*. For any  $u \in V(T)$ ,  $T[u]$  denotes the subtree of  $T$  rooted at the node  $u$ . Observe that if  $u$  is the root of  $T$  or if  $u$  is a leaf then  $\Lambda(T[u])$  is a trivial cluster. The set  $\mathcal{C}(T) = \bigcup_{u \in V(T)} \{\Lambda(T[u])\}$  is called the *cluster collection of  $T$* , and any cluster  $C \subseteq \Lambda(T)$  is said to *occur in  $T$*  if  $C \in \mathcal{C}(T)$ .

Two clusters  $C_1, C_2 \subseteq \Lambda(T)$  are *compatible* if  $C_1 \subseteq C_2$ ,  $C_2 \subseteq C_1$ , or  $C_1 \cap C_2 = \emptyset$ . If  $C_1$  and  $C_2$  are compatible, we write  $C_1 \smile C_2$ ; otherwise,  $C_1 \not\smile C_2$ . A cluster  $C \subseteq \Lambda(T)$  is *compatible with  $T$*  if  $C \smile \Lambda(T[u])$  holds for every node  $u \in V(T)$ . In this case, we write  $C \smile T$ , and  $C \not\smile T$  otherwise. If  $T_1$  and  $T_2$  are two trees with  $\Lambda(T_1) = \Lambda(T_2)$  such that every cluster in  $\mathcal{C}(T_1)$  is compatible with  $T_2$  then it follows that every cluster in  $\mathcal{C}(T_2)$  is compatible with  $T_1$ , and we say that  $T_1$  and  $T_2$  are *compatible*. Any two clusters or trees that are not compatible are called *incompatible*.

Next, let  $\mathcal{S} = \{T_1, T_2, \dots, T_k\}$  be a set of trees satisfying  $\Lambda(T_1) = \Lambda(T_2) = \dots = \Lambda(T_k) = L$  for some leaf label set  $L$ . For any cluster  $C$  of  $L$ , denote the set of all trees in  $\mathcal{S}$  in which  $C$  occurs by  $K_C(\mathcal{S})$  and the set of all trees in  $\mathcal{S}$  that are incompatible with  $C$  by  $Q_C(\mathcal{S})$ . Thus,  $K_C(\mathcal{S}) = \{T_i : C \in \mathcal{C}(T_i)\}$  and  $Q_C(\mathcal{S}) = \{T_i : C \not\smile T_i\}$ . Define three special types of clusters:

- If  $|K_C(\mathcal{S})| > \frac{k}{2}$  then  $C$  is a *majority cluster of  $\mathcal{S}$* .
- If  $|K_C(\mathcal{S})| > |Q_C(\mathcal{S})|$  then  $C$  is a *majority (+) cluster of  $\mathcal{S}$* .
- If  $|K_C(\mathcal{S})| > \max\{|K_D(\mathcal{S})| : D \subseteq L \text{ and } C \not\smile D\}$  then  $C$  is a *frequency difference cluster of  $\mathcal{S}$* .

(Informally, a frequency difference cluster is a cluster that occurs more frequently than each of the clusters that is incompatible with it.) Note that a majority cluster of  $\mathcal{S}$  is always a majority (+) cluster of  $\mathcal{S}$  and that a majority (+) cluster of  $\mathcal{S}$  is always a frequency difference cluster of  $\mathcal{S}$ , but not the other way around.

The *majority rule consensus tree of  $\mathcal{S}$*  [21] is the tree  $T$  such that  $\Lambda(T) = L$  and  $\mathcal{C}(T)$  consists of all majority clusters of  $\mathcal{S}$ . Similarly, the *majority rule (+) consensus tree of  $\mathcal{S}$*  [7, 11] is the tree  $T$  such that  $\Lambda(T) = L$  and  $\mathcal{C}(T)$  consists of all majority (+) clusters of  $\mathcal{S}$ , and the *frequency difference consensus tree of  $\mathcal{S}$*  [14] is the tree  $T$  such that  $\Lambda(T) = L$  and  $\mathcal{C}(T)$  consists of all frequency difference clusters of  $\mathcal{S}$ . See Fig. 1 for some examples.

From here on,  $\mathcal{S}$  is assumed to be an input set of identically leaf-labeled trees, and the leaf label set of  $\mathcal{S}$  is denoted by  $L$ . To express the size of the input, we define  $k = |\mathcal{S}|$  and  $n = |L|$ .

## 1.2 Previous Work

Margush and McMorris [21] introduced the majority rule consensus tree in 1981, and a deterministic algorithm for constructing it in optimal  $O(kn)$  worst-case running time was presented recently in [18]. (A randomized algorithm with  $O(kn)$  expected running time and unbounded worst-case running time was given earlier by Amenta *et al.* [2].) The majority rule consensus tree has several desirable mathematical properties [3, 16, 22], and algorithms for constructing it

have been implemented in popular computational phylogenetics packages like PHYLIP [13], TNT [15], COMPONENT [23], MrBayes [24], SumTrees in DendroPy [26], and PAUP\* [28]. Consequently, it is one of the most widely used consensus trees in practice [7, p. 450]. One drawback of the majority rule consensus tree is that it may be too harsh and discard valuable branching information. For example, in Fig. 1, even though the cluster  $\{a, b, c, d\}$  is compatible with 75% of the input trees, it is not included in the majority rule consensus tree. For this reason, people have become interested in alternative types of consensus trees that include all the majority clusters and at the same time, also include other meaningful, well-defined kinds of clusters. The majority rule (+) consensus tree and the frequency difference consensus tree are two such consensus trees.

The majority rule (+) consensus tree was defined by Dong *et al.* [11] in 2010. It was obtained as a special case of an attempted generalization by Cotton and Wilkinson [7] of the majority rule consensus tree. According to [11], Cotton and Wilkinson [7] suggested two types of supertrees<sup>1</sup> called majority-rule (-) and majority-rule (+) that were supposed to generalize the majority rule consensus tree. Unexpectedly, only the first one did, and by restricting the second one to the consensus tree case, [11] arrived at the majority rule (+) consensus tree. Dong *et al.* [11] established some fundamental properties of this type of consensus tree and pointed out the existence of a polynomial-time algorithm for constructing it, but left the task of finding the best possible such algorithm as an open problem. As far as we know, no implementation for computing the majority rule (+) consensus tree is publicly available.

Goloboff *et al.* [14] initially proposed the frequency difference consensus tree as a way to improve methods for evaluating group support in parsimony analysis. Its relationships to other consensus trees have been studied in [11]. A method for constructing it has been implemented in the free software package TNT [15] but the algorithm used is not documented and its time complexity is unknown. We note that since the number of clusters occurring in  $\mathcal{S}$  may be  $\Omega(kn)$ , a naive algorithm that compares every cluster in  $\mathcal{S}$  to every other cluster in  $\mathcal{S}$  directly would require  $\Omega(k^2n^2)$  time.

### 1.3 Organization of the Paper and New Results

Due to space constraints, some proofs have been omitted from the conference version of this paper. Please see the journal version for the complete proofs.

The paper is organized as follows. Section 2 summarizes some results from the literature that are needed later. In Section 3, we modify the techniques from [18] to obtain an  $O(kn)$ -time algorithm for the majority rule (+) consensus tree. Its running time is optimal because the size of the input is  $\Omega(kn)$ ; hence, we resolve the open problem of Dong *et al.* [11] mentioned above. Next, Section 4 gives a  $\min\{O(kn^2), O(kn(k + \log^2 n))\}$ -time algorithm for constructing the frequency difference consensus tree (here, the second term is smaller than the first term

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<sup>1</sup> A *supertree* is a generalization of a consensus tree that does not require the input trees to have identical leaf label sets.

if  $k = o(n)$ ; e.g., if  $k = O(1)$  then the running time reduces to  $O(n \log^2 n)$ . Our algorithms are fully deterministic and do not need to use hashing. Finally, Section 5 discusses implementations.

## 2 Preliminaries

### 2.1 The *delete* and *insert* Operations

The *delete* and *insert* operations are two operations that modify the structure of a tree. They are defined in the following way.

Let  $T$  be a tree and let  $u$  be any non-root, internal node in  $T$ . The *delete* operation on  $u$  makes all of  $u$ 's children become children of the parent of  $u$ , and then removes  $u$  and the edge between  $u$  and its parent. (See, e.g., Figure 2 in [17] for an illustration.) The time needed for this operation is proportional to the number of children of  $u$ , and the effect of applying it is that the cluster collection of  $T$  is changed to  $\mathcal{C}(T) \setminus \{\Lambda(T[u])\}$ . Conversely, the *insert* operation creates a new node  $u$  that becomes: (1) a child of an existing internal node  $v$ , and (2) the parent of a proper subset  $X$  of  $v$ 's children satisfying  $|X| \geq 2$ ; the effect is that  $\mathcal{C}(T)$  is changed to  $\mathcal{C}(T) \cup \{\Lambda(T[u])\}$ , where  $\Lambda(T[u]) = \bigcup_{v_i \in X} \Lambda(T[v_i])$ .

### 2.2 Subroutines

The new algorithms in this paper use the following algorithms from the literature as subroutines: Day's algorithm [9], Procedure `One-Way-Compatible` [17], and Procedure `Merge-Trees` [17]. Day's algorithm [9] is used to efficiently check whether any specified cluster that occurs in a tree  $T$  also occurs in another tree  $T_{ref}$ , and can be applied to find the set of all clusters that occur in both  $T$  and  $T_{ref}$  in linear time. Procedure `One-Way-Compatible` takes as input two trees  $T_A$  and  $T_B$  with identical leaf label sets and outputs a copy of  $T_A$  in which every cluster that is not compatible with  $T_B$  has been removed. (The procedure is asymmetric; e.g., if  $T_A$  consists of  $n$  leaves attached to a root node and  $T_B \neq T_A$  then `One-Way-Compatible`( $T_A, T_B$ ) =  $T_A$ , while `One-Way-Compatible`( $T_B, T_A$ ) =  $T_B$ .) Procedure `Merge-Trees` takes as input two compatible trees with identical leaf label sets and outputs a tree that combines their cluster collections. Their properties are summarized below; for details, see references [9] and [17].

**Lemma 1.** (*Day [9]*) Let  $T_{ref}$  and  $T$  be two given trees with  $\Lambda(T_{ref}) = \Lambda(T) = L$  and let  $n = |L|$ . After  $O(n)$  time preprocessing, it is possible to determine, for any  $u \in V(T)$ , if  $\Lambda(T[u]) \in \mathcal{C}(T_{ref})$  in  $O(1)$  time.

**Lemma 2.** (*[17]*) Let  $T_A$  and  $T_B$  be two given trees with  $\Lambda(T_A) = \Lambda(T_B) = L$  and let  $n = |L|$ . Procedure `One-Way-Compatible`( $T_A, T_B$ ) returns a tree  $T$  with  $\Lambda(T) = L$  such that  $\mathcal{C}(T) = \{C \in \mathcal{C}(T_A) : C \text{ is compatible with } T_B\}$  in  $O(n)$  time.

**Lemma 3.** (*[17]*) Let  $T_A$  and  $T_B$  be two given trees with  $\Lambda(T_A) = \Lambda(T_B) = L$  that are compatible and let  $n = |L|$ . Procedure `Merge-Trees`( $T_A, T_B$ ) returns a tree  $T$  with  $\Lambda(T) = L$  and  $\mathcal{C}(T) = \mathcal{C}(T_A) \cup \mathcal{C}(T_B)$  in  $O(n)$  time.

### 3 Constructing the Majority Rule (+) Consensus Tree

This section presents an algorithm named `Maj_Rule_Plus` for computing the majority rule (+) consensus tree of  $\mathcal{S}$  in (optimal)  $O(kn)$  time.

The pseudocode of `Maj_Rule_Plus` is given in Fig. 2. The algorithm has two phases. Phase 1 examines the input trees, one by one, to construct a set of candidate clusters that includes all majority (+) clusters. Then, Phase 2 removes all candidate clusters that are not majority (+) clusters.<sup>2</sup>

During Phase 1, the current candidate clusters are stored as nodes in a tree  $T$ . Every node  $v$  in  $T$  represents a current candidate cluster  $\Lambda(T[v])$  and has a counter  $count(v)$  that, starting from the iteration at which  $\Lambda(T[v])$  became a candidate cluster, keeps track of the number of input trees in which it occurs minus the number of input trees that are incompatible with it. More precisely, while treating the tree  $T_j$  for any  $j \in \{2, 3, \dots, k\}$  in Step 3.1,  $count(v)$  for each current candidate cluster  $\Lambda(T[v])$  is updated as follows: if  $\Lambda(T[v])$  occurs in  $T_j$  then  $count(v)$  is incremented by 1, if  $\Lambda(T[v])$  does not occur in  $T_j$  and is not compatible with  $T_j$  then  $count(v)$  is decremented by 1, and otherwise (i.e.,  $\Lambda(T[v])$  does not occur in  $T_j$  but is compatible with  $T_j$ )  $count(v)$  is unchanged. Furthermore, if any  $count(v)$  reaches 0 then the node  $v$  is deleted from  $T$  so that  $\Lambda(T[v])$  is no longer a current candidate cluster. Next, in Step 3.3, every cluster occurring in  $T_j$  that is not a current candidate but compatible with  $T$  is inserted into  $T$  (thus becoming a current candidate cluster) and its counter is initialized to 1. Lemma 4 below proves that the set of majority (+) clusters of  $\mathcal{S}$  is contained in the set of candidate clusters at the end of Phase 1.

**Lemma 4.** *For any  $C \subseteq L$ , if  $C$  is a majority (+) cluster of  $\mathcal{S}$  then  $C \in \mathcal{C}(T)$  at the end of Phase 1.*

*Proof.* Suppose that  $C$  is a majority (+) cluster of  $\mathcal{S}$ . Let  $T_x$  be any tree in  $Q_C(\mathcal{S})$  and consider iteration  $x$  in Step 3: If  $C$  is a current candidate at the beginning of iteration  $x$  then its counter will be decremented, cancelling out the occurrence of  $C$  in one tree  $T_j$  where  $1 \leq j < x$ ; otherwise,  $C$  may be prevented from being inserted into  $T$  in at most one later iteration  $j$  (where  $x < j \leq k$  and  $C \in \mathcal{C}(T_j)$ ) because of some cluster occurring in  $T_x$ . It follows from  $|K_C(\mathcal{S})| - |Q_C(\mathcal{S})| > 0$  that  $C$ 's counter will be greater than 0 at the end of Phase 1, and therefore  $C \in \mathcal{C}(T)$ .  $\square$

In Phase 2, Step 5 of the algorithm computes the values of  $|K_C(\mathcal{S})|$  and  $|Q_C(\mathcal{S})|$  for every candidate cluster  $C$  and stores them in  $K(v)$  and  $Q(v)$ , respectively, where  $C = \Lambda(T[v])$ . Finally, Step 6 removes every candidate cluster  $C$  that does not satisfy the condition  $|K_C(\mathcal{S})| > |Q_C(\mathcal{S})|$ . By definition, the clusters that remain in  $T$  are the majority rule (+) clusters.

**Theorem 1.** *Algorithm `Maj_Rule_Plus` constructs the majority rule (+) consensus tree of  $\mathcal{S}$  in  $O(kn)$  time.*

<sup>2</sup> This basic strategy was previously used in the  $O(kn)$ -time algorithm in [18] for computing the majority rule consensus tree.

**Algorithm** Maj\_Rule\_Plus**Input:** A set  $\mathcal{S} = \{T_1, T_2, \dots, T_k\}$  of trees with  $\Lambda(T_1) = \Lambda(T_2) = \dots = \Lambda(T_k)$ .**Output:** The majority rule (+) consensus tree of  $\mathcal{S}$ .

```

/* Phase 1 */
1   $T := T_1$ 
2  for each  $v \in V(T)$  do  $count(v) := 1$ 
3  for  $j := 2$  to  $k$  do
3.1  for each  $v \in V(T)$  do
      if  $\Lambda(T[v])$  occurs in  $T_j$  then  $count(v) := count(v) + 1$ 
      else if  $\Lambda(T[v])$  is not compatible with  $T_j$  then  $count(v) := count(v) - 1$ 
    endfor
3.2  for each  $v \in V(T)$  in top-down order do
      if  $count(v) = 0$  then delete node  $v$ .
    endfor
3.3  for every  $C \in \mathcal{C}(T_j)$  that is compatible with  $T$  but does not occur in  $T$  do
      Insert  $C$  into  $T$ .
      Initialize  $count(v) := 1$  for the new node  $v$  satisfying  $\Lambda(T[v]) = C$ .
    endfor
endfor

/* Phase 2 */
4  for each  $v \in V(T)$  do  $K(v) := 0$ ;  $Q(v) := 0$ 
5  for  $j := 1$  to  $k$  do
5.1  for each  $v \in V(T)$  do
      if  $\Lambda(T[v])$  occurs in  $T_j$  then  $K(v) := K(v) + 1$ 
      else if  $\Lambda(T[v])$  is not compatible with  $T_j$  then  $Q(v) := Q(v) + 1$ 
    endfor
6  for each  $v \in V(T)$  in top-down order do
      if  $K(v) \leq Q(v)$  then perform a delete operation on  $v$ .
    endfor
7  return  $T$ 
End Maj_Rule_Plus

```

**Fig. 2.** Algorithm Maj\_Rule\_Plus for constructing the majority rule (+) consensus tree

*Proof.* The correctness follows from Lemma 4 and the above discussion.

The time complexity analysis is analogous to the proof of Theorem 4 in [18]. First consider Phase 1. Step 3.1 takes  $O(n)$  time by: (1) running Day's algorithm with  $T_{ref} = T_j$  and then checking each node  $v$  in  $V(T)$  to see if  $\Lambda(T[v])$  occurs in  $T_j$  (according to Lemma 1, this requires  $O(n)$  time for preprocessing, and each of the  $O(n)$  nodes in  $V(T)$  may be checked in  $O(1)$  time), and (2) computing  $X := \text{One-Way-Compatible}(T, T_j)$  and then checking for each node  $v$  in  $V(T)$  if  $v$  does not exist in  $X$  to determine if  $\Lambda(T[v]) \not\sim T_j$  (this takes  $O(n)$  time by Lemma 2). The *delete* operations in Step 3.2 take  $O(n)$  time because the nodes are handled in top-down order, which means that for every node, its parent will change at most once in each iteration. In Step 3.3, define  $Y := \text{One-Way-Compatible}(T_j, T)$  and  $Z := \text{Merge-Trees}(Y, T)$ . Then by Lemmas 2

and 3, the cluster collection of  $Y$  consists of the clusters occurring in  $T_j$  that are compatible with the set of current candidates, and  $Z$  is the result of inserting these clusters into  $T$ . Thus, Step 3.3 can be implemented by computing  $Y$  and  $Z$ , updating  $T$ 's structure according to  $Z$ , and setting the counters of all new nodes to 1, so Step 3.3 takes  $O(n)$  time. The main loop in Step 3 consists of  $O(k)$  iterations, and Phase 1 therefore takes  $O(kn)$  time in total.

Next, Phase 2 also takes  $O(kn)$  time because Step 5.1 can be implemented in  $O(n)$  time with the same techniques as in Step 3.1, and Step 6 is performed in  $O(n)$  time by handling the nodes in top-down order so that each node's parent is changed at most once, as in Step 3.2.  $\square$

## 4 Constructing the Frequency Difference Consensus Tree

Here, we present an algorithm for finding the frequency consensus tree of  $\mathcal{S}$  in  $\min\{O(kn^2), O(kn(k + \log^2 n))\}$  time. It is called `FrequencyDifference` and is described in Section 4.1 below. The algorithm uses the procedure `Merge_Trees` as well as a new procedure named `Filter_Clusters` whose details are given in Section 4.2.

For each tree  $T_j \in \mathcal{S}$  and each node  $u \in V(T_j)$ , define the *weight of  $u$*  as the value  $|K_{\Lambda(T_j[u])}(\mathcal{S})|$ , i.e., the number of trees from  $\mathcal{S}$  in which the cluster  $\Lambda(T_j[u])$  occurs, and denote it by  $w(u)$ . For convenience, also define  $w(C) = w(u)$ , where  $C = \Lambda(T_j[u])$ . The input to Procedure `Filter_Clusters` is two trees  $T_A, T_B$  with  $\Lambda(T_A) = \Lambda(T_B) = L$  such that every cluster occurring in  $T_A$  or  $T_B$  also occurs in at least one tree in  $\mathcal{S}$ , and the output is a copy of  $T_A$  in which every cluster that is incompatible with some cluster in  $T_B$  with a higher weight has been removed. Formally, the output of `Filter_Clusters` is a tree  $T$  with  $\Lambda(T) = L$  such that  $\mathcal{C}(T) = \{\Lambda(T_A[u]) : u \in V(T_A) \text{ and } w(u) > w(x) \text{ for every } x \in V(T_B) \text{ with } \Lambda(T_A[u]) \not\prec \Lambda(T_B[x])\}$ .

### 4.1 Algorithm `FrequencyDifference`

We first describe Algorithm `FrequencyDifference`. Refer to Fig. 3 for the pseudocode.

The algorithm starts by computing the weight  $w(C)$  of every cluster  $C$  occurring in  $\mathcal{S}$  in a preprocessing step (Step 1). Next, let  $\mathcal{C}(S)$  for any set  $S$  of trees denote the union  $\bigcup_{T_i \in S} \mathcal{C}(T_i)$ , and for any  $j \in \{1, 2, \dots, k\}$ , define a *forward frequency difference consensus tree of  $\{T_1, T_2, \dots, T_j\}$*  as any tree that includes every cluster  $C$  in  $\mathcal{C}(\{T_1, T_2, \dots, T_j\})$  satisfying  $w(C) > w(X)$  for all  $X \in \mathcal{C}(\{T_1, T_2, \dots, T_j\})$  with  $C \not\prec X$ . Steps 2–3 use Procedure `Filter_Clusters` from Section 4.2 to build a tree  $T$  that, after any iteration  $j \in \{1, 2, \dots, k\}$ , is a forward frequency difference consensus tree of  $\{T_1, T_2, \dots, T_j\}$ , as proved in Lemma 5 below. After iteration  $k$ ,  $\mathcal{C}(T)$  contains all frequency difference clusters of  $\mathcal{S}$  but possibly some other clusters as well, so Step 4 applies `Filter_Clusters` again to remove all non-frequency difference clusters of  $\mathcal{S}$  from  $T$ .

```

Algorithm   Frequency_Difference
Input:    A set  $\mathcal{S} = \{T_1, T_2, \dots, T_k\}$  of trees with  $A(T_1) = A(T_2) = \dots = A(T_k)$ .
Output:  The frequency difference consensus tree of  $\mathcal{S}$ .

    /* Preprocessing */
    1 Compute  $w(C)$  for every cluster  $C$  occurring in  $\mathcal{S}$ .

    /* Main algorithm */
    2  $T := T_1$ 
    3 for  $j := 2$  to  $k$  do
         $A := \text{Filter\_Clusters}(T, T_j)$ ;  $B := \text{Filter\_Clusters}(T_j, T)$ 
         $T := \text{Merge\_Trees}(A, B)$ 
    endfor
    4 for  $j := 1$  to  $k$  do  $T := \text{Filter\_Clusters}(T, T_j)$ 
    5 return  $T$ 
End   Frequency_Difference
    
```

**Fig. 3.** Algorithm Frequency\_Difference for constructing the frequency difference consensus tree

**Lemma 5.** For any  $j \in \{2, 3, \dots, k\}$ , suppose that  $T$  is a forward frequency difference consensus tree of  $\{T_1, T_2, \dots, T_{j-1}\}$ . Let  $A := \text{Filter\_Clusters}(T, T_j)$  and  $B := \text{Filter\_Clusters}(T_j, T)$ . Then  $\text{Merge\_Trees}(A, B)$  is a forward frequency difference consensus tree of  $\{T_1, T_2, \dots, T_j\}$ .

*Proof.* (Omitted from the conference version due to space constraints.) □

**Theorem 2.** Algorithm Frequency\_Difference constructs the frequency difference consensus tree of  $\mathcal{S}$  in  $\min\{O(kn^2), O(k^2n)\} + O(k \cdot f(n))$  time, where  $f(n)$  is the running time of Procedure Filter\_Clusters.

*Proof.* After completing iteration  $k$  of Step 3,  $\mathcal{C}(T)$  is a superset of the set of all frequency difference clusters of  $\mathcal{S}$  by Lemma 5. Next, Step 4 removes all non-frequency difference clusters of  $\mathcal{S}$ , so the output will be the frequency difference consensus tree of  $\mathcal{S}$ .

To analyze the time complexity, first consider how to compute all the weights in Step 1. One method is to first fix an arbitrary ordering of  $L$  and represent every cluster  $C$  of  $L$  as a bit vector of length  $n$  (for every  $i \in \{1, 2, \dots, n\}$ , the  $i$ th bit is set to 1 if and only if the  $i$ th leaf label belongs to  $C$ ). Then, spend  $O(kn^2)$  time to construct a list of bit vectors for all  $O(kn)$  clusters occurring in  $\mathcal{S}$  by a bottom-up traversal of each tree in  $\mathcal{S}$ , sort the resulting list of bit vectors by radix sort, and traverse the sorted list to identify the number of occurrences of each cluster. All this takes  $O(kn^2)$  time. An alternative method, which uses  $O(k^2n)$  time, is to initialize the weight of every node in  $\mathcal{S}$  to 1 and then, for  $j \in \{1, 2, \dots, k\}$ , apply Day’s algorithm (see Lemma 1) with  $T_{ref} = T_j$  and  $T$  ranging over all  $T_i$  with  $1 \leq i \leq k, i \neq j$  to find all clusters in  $T$  that also occur in  $T_j$  and increase the

weights of their nodes in  $T$  by 1. Therefore, Step 1 takes  $\min\{O(kn^2), O(k^2n)\}$  time. Next, Steps 3 and 4 make  $O(k)$  calls to the procedures `Merge_Trees` and `Filter_Clusters`. The running time of `Merge_Trees` is  $O(n)$  by Lemma 3 and the running time of `Filter_Clusters` is  $f(n) = \Omega(n)$ , so Steps 3 and 4 take  $O(k \cdot f(n))$  time.  $\square$

Lemma 7 in the next subsection shows that  $f(n) = O(n \log^2 n)$  is possible, which yields:

**Corollary 1.** *Algorithm `Frequency_Difference` constructs the frequency difference consensus tree of  $\mathcal{S}$  in  $\min\{O(kn^2), O(kn(k + \log^2 n))\}$  time.*

## 4.2 Procedure `Filter_Clusters`

Recall that for any node  $u$  in any input tree  $T_j$ , its weight  $w(u)$  is  $|K_{\Lambda(T_j[u])}(\mathcal{S})|$ . Also,  $w(C) = w(u)$ , where  $C = \Lambda(T_j[u])$ . We assume that all  $w(u)$ -values have been computed in a preprocessing step and are available.

Let  $T$  be a tree. For every nonempty  $X \subseteq V(T)$ ,  $\text{lca}^T(X)$  denotes the lowest common ancestor of  $X$  in  $T$ . To obtain a fast solution for `Filter_Clusters`, we need the next lemma.

**Lemma 6.** *Let  $T$  be a tree, let  $X$  be any cluster of  $\Lambda(T)$ , and let  $r_X = \text{lca}^T(X)$ . For any  $v \in V(T)$ , it holds that  $X \not\prec \Lambda(T[v])$  if and only if: (1)  $v$  lies on a path from a child of  $r_X$  to some leaf belonging to  $X$ ; and (2)  $\Lambda(T[v]) \not\subseteq X$ .*

*Proof.* Given  $T$ ,  $X$ ,  $r_X$ , and  $v$  as in the lemma statement, there are four possible cases: (i)  $v$  is a proper ancestor of  $r_X$  or equal to  $r_X$ ; (ii)  $v$  lies on a path from a child of  $r_X$  to some leaf in  $X$  and all leaf descendants of  $v$  belong to  $X$ ; (iii)  $v$  lies on a path from a child of  $r_X$  to some leaf in  $X$  and not all leaf descendants of  $v$  belong to  $X$ ; or (iv)  $v$  is a proper descendant of  $r_X$  that does not lie on any path from a leaf in  $X$  to  $r_X$ . In case (i),  $X \subseteq \Lambda(T[v])$ . In case (ii),  $\Lambda(T[v]) \subseteq X$ . In case (iii),  $\Lambda(T[v]) \not\subseteq X$  while  $X \cap \Lambda(T[v]) \neq \emptyset$ . In case (iv),  $X \cap \Lambda(T[v]) = \emptyset$ . By the definition of compatible clusters,  $X \not\prec \Lambda(T[v])$  if and only if case (iii) occurs.  $\square$

Lemma 6 leads to an  $O(n^2)$ -time method for `Filter_Clusters`, which we now briefly describe. For each node  $u \in V(T_A)$  in top-down order, do the following: Let  $X = \Lambda(T_A[u])$  and find all  $v \in V(T_B)$  such that  $X \not\prec \Lambda(T_B[v])$  in  $O(n)$  time by doing bottom-up traversals of  $T_B$  to first mark all ancestors of leaves belonging to  $X$  that are proper descendants of the lowest common ancestor of  $X$  in  $T_B$ , and then unmarking all marked nodes that have no leaf descendants outside of  $X$ . By Lemma 6,  $X \not\prec \Lambda(T_B[v])$  if and only if  $v$  is one of the resulting marked nodes. If  $w(u) \leq w(v)$  for any such  $v$  then do a *delete* operation on  $u$  in  $T_A$ . Clearly, the total running time is  $O(n^2)$ . (This simple method gives  $f(n) = O(n^2)$  in Theorem 2 in Section 4.1, and hence a total running time of  $O(kn^2)$  for Algorithm `Frequency_Difference`.) Below, we refine this idea to get an even faster solution for `Filter_Clusters`.

**High-Level Description.** We use the *centroid path decomposition* technique [6] to divide the nodes of  $T_A$  into a so-called centroid path and a set of side trees. A *centroid path* of  $T_A$  is defined as a path in  $T_A$  of the form  $\pi = \langle p_\alpha, p_{\alpha-1}, \dots, p_1 \rangle$ , where  $p_\alpha$  is the root of  $T_A$ , the node  $p_{i-1}$  for every  $i \in \{2, \dots, \alpha\}$  is any child of  $p_i$  with the maximum number of leaf descendants, and  $p_1$  is a leaf. Given a centroid path  $\pi$ , removing  $\pi$  and all its incident edges from  $T_A$  produces a set  $\sigma(\pi)$  of disjoint trees whose root nodes are children of nodes belonging to  $\pi$  in  $T_A$ ; these trees are called the *side trees* of  $\pi$ . Importantly,  $|\Lambda(\tau)| \leq n/2$  for every side tree  $\tau$  of  $\pi$ . Also,  $\{\Lambda(\tau) : \tau \in \sigma(\pi)\}$  forms a partition of  $L \setminus \{p_1\}$ . Furthermore, if  $\pi$  is a centroid path of  $T_A$  then the cluster collection  $\mathcal{C}(T_A)$  can be written recursively as  $\mathcal{C}(T_A) = \bigcup_{\tau \in \sigma(\pi)} \mathcal{C}(\tau) \cup \bigcup_{p_i \in \pi} \{\Lambda(T_A[p_i])\}$ . Intuitively, this allows the cluster collection of  $T_A$  to be broken into smaller sets that can be checked more easily, and then put together again at the end.

The fast version of `Filter_Clusters` is shown in Fig. 4. It first computes a centroid path  $\pi = \langle p_\alpha, p_{\alpha-1}, \dots, p_1 \rangle$  of  $T_A$  and the set  $\sigma(\pi)$  of side trees of  $\pi$  in Step 1. Then, in Steps 2–3, it applies itself recursively to each side tree of  $\pi$  to get rid of any cluster in  $\bigcup_{\tau \in \sigma(\pi)} \mathcal{C}(\tau)$  that is incompatible with some cluster in  $T_B$  with a higher weight than itself, and the remaining clusters are inserted into a temporary tree  $R_s$ . Next, Steps 4–5 check all clusters in  $\bigcup_{p_i \in \pi} \{\Lambda(T_A[p_i])\}$  to determine which of them are not incompatible with any cluster in  $T_B$  with a higher weight, and create a temporary tree  $R_c$  whose cluster collection consists of all those clusters that pass this test. Finally, Step 6 combines the cluster collections of  $R_s$  and  $R_c$  by applying the procedure `Merge_Trees`. The details of Procedure `Filter_Clusters` are discussed next.

**Steps 2–3 (Handling the Side Trees).** For every nonempty  $C \subseteq \Lambda(T)$ , define  $T|C$  (“the subtree of  $T$  induced by  $C$ ”; see, e.g., [6]) as the tree  $T'$  with leaf label set  $C$  and internal node set  $\{lca^T(\{a, b\}) : a, b \in C\}$  which preserves the ancestor relations from  $T$ , i.e., which satisfies  $lca^T(C') = lca^{T'}(C')$  for all nonempty  $C' \subseteq C$ . Now, let  $\sigma(\pi)$  be the set of side trees of the centroid path  $\pi$  computed in Step 1. For each  $\tau \in \sigma(\pi)$ , define a weighted tree  $T_B|\Lambda(\tau)$  as follows. First, construct  $T_B|\Lambda(\tau)$  and let the weight of each node in this tree equal its weight in  $T_B$ . Next, for each edge  $(u, v)$  in  $T_B|\Lambda(\tau)$ , let  $P$  be the path in  $T_B$  between  $u$  and  $v$ , excluding  $u$  and  $v$ ; if  $P$  is not empty then create a new node  $z$  in  $T_B|\Lambda(\tau)$ , replace the edge  $(u, v)$  by the two edges  $(u, z)$  and  $(z, v)$ , and set the weight of  $z$  to the maximum weight of all nodes belonging to  $P$ . Each such  $z$  is called a *special node* and has exactly one child. See Fig. 5 for an example. We extend the concept of “compatible” to special nodes as follows: if  $C \subseteq L$  and  $z$  is a special node in  $T_B|\Lambda(\tau)$  then  $C \smile z$  if and only if  $C$  and  $\Lambda((T_B|\Lambda(\tau))[z])$  are disjoint or  $(T_B|\Lambda(\tau))[z]$  has no proper descendant that is a special node. The obtained tree  $T_B|\Lambda(\tau)$  satisfies  $\Lambda(\tau) = \Lambda(T_B|\Lambda(\tau))$  and has the property that for every cluster  $C$  in  $\mathcal{C}(\tau)$ ,  $\max\{w(X) : X \in \mathcal{C}(T_B) \text{ and } C \not\smile X\}$  is equal to  $\max\{w(X) : X \in \mathcal{C}(T_B|\Lambda(\tau)) \text{ and } C \not\smile X\}$ .

After constructing  $T_B|\Lambda(\tau)$ , `Filter_Clusters` is applied to  $(\tau, T_B|\Lambda(\tau))$  recursively to remove all bad clusters from  $\tau$ . For each  $\tau \in \sigma(\pi)$ , the resulting tree is denoted by  $\tau'$ . All the clusters of  $\tau'$  are inserted into the tree  $R_s$  by

**Algorithm** Filter\_Clusters

**Input:** Two trees  $T_A, T_B$  with  $\Lambda(T_A) = \Lambda(T_B) = L$  such that every cluster occurring in  $T_A$  or  $T_B$  also occurs in at least one tree in  $\mathcal{S}$ .

**Output:** A tree  $T$  with  $\Lambda(T) = L$  such that  $\mathcal{C}(T) = \{\Lambda(T_A[u]) : u \in V(T_A) \text{ and } w(u) > w(x) \text{ for every } x \in V(T_B) \text{ with } \Lambda(T_A[u]) \not\prec \Lambda(T_B[x])\}$ .

1 Compute a centroid path  $\pi = \langle p_\alpha, p_{\alpha-1}, \dots, p_1 \rangle$  of  $T_A$ , where  $p_\alpha$  is the root of  $T_A$  and  $p_1$  is a leaf, and compute the set  $\sigma(\pi)$  of side trees of  $\pi$ .

/\* Handle the side trees. \*/

2 Let  $R_s$  be a tree consisting only of a root node and a single leaf labeled by  $p_1$ .

3 **for** each side tree  $\tau \in \sigma(\pi)$  **do**

$\tau' := \text{Filter\_Clusters}(\tau, T_B | \Lambda(\tau))$

    Attach the root of  $\tau'$  to the root of  $R_s$ .

**endfor**

/\* Handle the centroid path. \*/

4 Let  $R_c$  be a tree with  $\Lambda(R_c) = L$  where every leaf is directly attached to the root. Let  $BT$  be an empty binary search tree. For every  $x \in V(T_B)$ , initialize  $counter(x) := 0$ . Do a bottom-up traversal of  $T_B$  to precompute  $|\Lambda(T_B[x])|$  for every  $x \in V(T_B)$ . Preprocess  $T_B$  for answering *lca*-queries. Let  $\beta_1 := 0$ .

5 **for**  $i := 2$  **to**  $\alpha$  **do**

5.1 Let  $D$  be the set of leaves in  $\Lambda(T_A[p_i]) \setminus \Lambda(T_A[p_{i-1}])$ .

5.2 Compute  $r_i := \text{lca}^{T_B}(\{r_{i-1}\} \cup D)$ . /\*  $r_i$  now equals  $\text{lca}^{T_B}(\Lambda(T_A[p_i])$ . \*/

5.3 Insert every node belonging to the path from  $r_i$  to  $r_{i-1}$ , except  $r_i$ , into  $BT$ .

5.4 **for** each  $x \in D$  **do**

    Insert  $x$  into  $BT$ .

**while** ( $\text{parent}(x)$  is not in  $BT$  and  $\text{parent}(x) \neq r_i$ ) **do**

$x := \text{parent}(x)$ ; insert  $x$  into  $BT$ .

**endfor**

5.5 **for** each  $x \in D$  **do**

$counter(x) := counter(x) + 1$

**while** ( $counter(x) = |\Lambda(T_B[x])|$ ) **do**

$counter(\text{parent}(x)) := counter(\text{parent}(x)) + |\Lambda(T_B[x])|$

        Remove  $x$  from  $BT$ ;  $x := \text{parent}(x)$

**endwhile**

**endfor**

5.6 Let  $M :=$  maximum weight of a node in  $BT$ ; **if**  $BT$  is empty **then**  $M := 0$ .

5.7 Compute  $\beta_i$ , and **if**  $\beta_i > M$  **then** let  $M := \beta_i$ .

5.8 **if** ( $w(\Lambda(T_A[p_i])) > M$ ) **then** put  $\Lambda(T_A[p_i])$  in  $R_c$  by an *insert* operation.

**endfor**

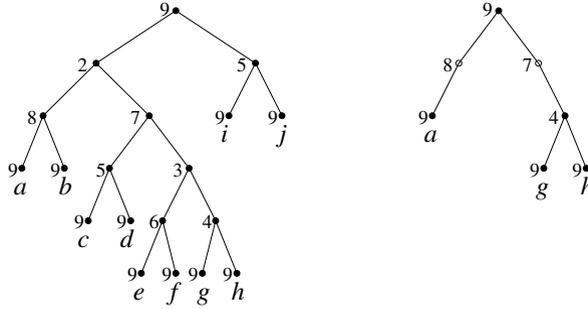
/\* Combine the surviving clusters. \*/

6  $T := \text{Merge\_Trees}(R_s, R_c)$

7 **return**  $T$

**End** Filter\_Clusters

**Fig. 4.** The procedure Filter\_Clusters



**Fig. 5.** Let  $T_B$  be the tree (with node weights) on the left. The tree  $T_B||\{a, g, h\}$  is shown on the right.

directly attaching  $\tau'$  to the root of  $R_s$ . Since  $\{\Lambda(\tau') : \tau \in \sigma(\pi)\}$  forms a partition of  $L \setminus \{p_1\}$ , every leaf label in  $L$  appears exactly once in  $R_s$  and we have  $\mathcal{C}(R_s) = \{\Lambda(T_A[u]) : u \in V(\tau) \text{ for some } \tau \in \sigma(\pi) \text{ and } w(u) > w(x) \text{ for every } x \in V(T_B) \text{ with } \Lambda(T_A[u]) \not\subseteq \Lambda(T_B[x])\} \cup \{L\}$  after Step 3 is finished.

**Steps 4–5 (Handling the Centroid Path).** The clusters  $\bigcup_{p_i \in \pi} \{\Lambda(T_A[p_i])\}$  on the centroid path are nested because  $p_i$  is the parent of  $p_{i-1}$ , so  $\Lambda(T_A[p_{i-1}]) \subseteq \Lambda(T_A[p_i])$  for every  $i \in \{2, 3, \dots, \alpha\}$ . The main loop (Step 5) checks each of these clusters in order of increasing cardinality.

The algorithm maintains a binary search tree  $BT$  that, right after Step 5.5 in any iteration  $i$  of the main loop is complete, contains every node  $x$  from  $T_B$  with  $\Lambda(T_A[p_i]) \not\subseteq \Lambda(T_B[x])$ . Whenever a node  $x$  is inserted into  $BT$ , its key is set to the weight  $w(T_B[x])$ . Using  $BT$ , Step 5.6 retrieves the weight  $M$  of the heaviest cluster in  $T_B$  that is incompatible with  $\Lambda(T_A[p_i])$  (if any). Then, Step 5.7 computes a value  $\beta_i$ , defined as the maximum weight of all special nodes in  $T_B$  (if any) that are incompatible with the current  $T_A[p_i]$ ; if  $\beta_i > M$  then  $M$  is set to  $\beta_i$ . Step 5.8 saves  $\Lambda(T_A[p_i])$  by inserting it into the tree  $R_c$  if its weight is strictly greater than  $M$ . After Step 5 is done,  $\mathcal{C}(R_c) = \{\Lambda(T_A[u]) : u \in \pi \text{ and } w(u) > w(x) \text{ for every } x \in V(T_B) \text{ with } \Lambda(T_A[u]) \not\subseteq \Lambda(T_B[x])\}$ .

In order to update  $BT$  correctly while moving upwards along  $\pi$  in Step 5, the algorithm relies on Lemma 6. In each iteration  $i \in \{2, 3, \dots, \alpha\}$  of Step 5,  $r_i$  is the lowest common ancestor in  $T_B$  of  $\Lambda(T_A[p_i])$ . By Lemma 6, the clusters in  $T_B$  that are incompatible with  $\Lambda(T_A[p_i])$  are of the form  $T_B[v]$  where: (1)  $v$  lies on a path in  $T_B$  from a child of  $r_i$  to a leaf in  $\Lambda(T_A[p_i])$ ; and (2)  $\Lambda(T[v]) \not\subseteq \Lambda(T_A[p_i])$ . Accordingly,  $BT$  is updated in Steps 5.3–5.5 as follows. Condition (1) is taken care of by first inserting all nodes from  $T_B$  between  $r_{i-1}$  and  $r_i$  except  $r_i$  into  $BT$  in Step 5.3 and then inserting all leaf descendants of  $p_i$  that are not descendants of  $p_{i-1}$ , along with any of their ancestors in  $T_B$  that were not already in  $BT$ , into  $BT$  in Step 5.4. Finally, Step 5.5 enforces condition (2) by using counters to locate and remove all nodes from  $BT$  (if any) whose clusters are proper subsets of  $\Lambda(T_A[p_i])$ . To do this,  $counter(x)$  for every node  $x$  in  $T_B$  is updated so that

it stores the number of leaves in  $\Lambda(T_B[x]) \cap \Lambda(T_A[p_i])$  for the current  $i$ , and if  $\text{counter}(x)$  reaches the value  $|\Lambda(T_B[x])|$  then  $x$  is removed from  $BT$ .

To compute  $\beta_i$  in Step 5.7, take the maximum of: (i)  $\beta_{i-1}$ ; (ii) the weights of all special nodes on the path between  $r_i$  and  $r_{i-1}$  in  $T_B$ ; and (iii) the weights of all special nodes that belong to a path between  $r_i$  and a leaf in  $D$ .

**Lemma 7.** *Procedure `Filter_Clusters` runs in  $O(n \log^2 n)$  time.*

*Proof.* (Omitted from the conference version due to space constraints.) □

## 5 Implementations

As noted in Section 1.2, there does not seem to be any publicly available implementation for the majority rule (+) consensus tree. To fill this void, we implemented Algorithm `Maj_Rule_Plus` from Section 3 in C++ and included it in the source code of the FACT (Fast Algorithms for Consensus Trees) package [17] at:

<http://compbio.ddns.comp.nus.edu.sg/~consensus.tree/>

To test the implementation, we repeatedly applied it to 10 random sets of trees for various specified values of  $(k, n)$ , generated with the method described in Section 6.2 of [17]. The following worst-case running times (in seconds) were obtained using Ubuntu Nutty Narwhal, a 64-bit operating system with 8.00 GB RAM, and a 2.20 GHz CPU:

$(k, n)$	(100, 500)	(100, 1000)	(100, 2000)	(100, 5000)	(500, 100)	(1000, 100)	(2000, 100)	(5000, 100)	(1000, 2000)
Time	0.63	1.51	2.99	6.78	0.65	1.29	2.72	6.66	27.29

The situation for the frequency difference consensus tree is less critical as there already exist implementations, e.g., in the software package TNT [15]. Nevertheless, it could be useful to implement our algorithm `Frequency_Difference` from Section 4 in the future and compare its practical performance to TNT. Before doing that, one should try to simplify the procedure `Filter_Clusters`.

## References

- Adams III, E.N.: Consensus techniques and the comparison of taxonomic trees. *Systematic Zoology* 21(4), 390–397 (1972)
- Amenta, N., Clarke, F., St. John, K.: A linear-time majority tree algorithm. In: Benson, G., Page, R.D.M. (eds.) WABI 2003. LNCS (LNBI), vol. 2812, pp. 216–227. Springer, Heidelberg (2003)
- Barthélemy, J.-P., McMorris, F.R.: The median procedure for  $n$ -trees. *Journal of Classification* 3(2), 329–334 (1986)
- Bremer, K.: Combinable component consensus. *Cladistics* 6(4), 369–372 (1990)
- Bryant, D.: A classification of consensus methods for phylogenetics. In: Janowitz, M.F., Lapointe, F.-J., McMorris, F.R., Mirkin, B., Roberts, F.S. (eds.) Bioconsensus. DIMACS Series in Discrete Mathematics and Theoretical Computer Science, vol. 61, pp. 163–184. American Mathematical Society (2003)
- Cole, R., Farach-Colton, M., Hariharan, R., Przytycka, T., Thorup, M.: An  $O(n \log n)$  algorithm for the maximum agreement subtree problem for binary trees. *SIAM Journal on Computing* 30(5), 1385–1404 (2000)

7. Cotton, J.A., Wilkinson, M.: Majority-rule supertrees. *Systematic Biology* 56(3), 445–452 (2007)
8. Cui, Y., Jansson, J., Sung, W.-K.: Polynomial-time algorithms for building a consensus MUL-tree. *Journal of Computational Biology* 19(9), 1073–1088 (2012)
9. Day, W.H.E.: Optimal algorithms for comparing trees with labeled leaves. *Journal of Classification* 2(1), 7–28 (1985)
10. Degnan, J.H., DeGiorgio, M., Bryant, D., Rosenberg, N.A.: Properties of consensus methods for inferring species trees from gene trees. *Systematic Biology* 58(1), 35–54 (2009)
11. Dong, J., Fernández-Baca, D., McMorris, F.R., Powers, R.C.: Majority-rule (+) consensus trees. *Mathematical Biosciences* 228(1), 10–15 (2010)
12. Felsenstein, J.: *Inferring Phylogenies*. Sinauer Associates, Inc., Sunderland (2004)
13. Felsenstein, J.: PHYLIP, version 3.6. Software package, Department of Genome Sciences. University of Washington, Seattle (2005)
14. Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J., Szumik, C.A.: Improvements to resampling measures of group support. *Cladistics* 19(4), 324–332 (2003)
15. Goloboff, P.A., Farris, J.S., Nixon, K.C.: TNT, a free program for phylogenetic analysis. *Cladistics* 24(5), 774–786 (2008)
16. Holder, M.T., Sukumaran, J., Lewis, P.O.: A justification for reporting the majority-rule consensus tree in Bayesian phylogenetics. *Systematic Biology* 57(5), 814–821 (2008)
17. Jansson, J., Shen, C., Sung, W.-K.: Improved algorithms for constructing consensus trees. In: *Proceedings of SODA 2013*, pp. 1800–1813. SIAM (2013)
18. Jansson, J., Shen, C., Sung, W.-K.: An optimal algorithm for building the majority rule consensus tree. In: Deng, M., Jiang, R., Sun, F., Zhang, X. (eds.) *RECOMB 2013*. LNCS, vol. 7821, pp. 88–99. Springer, Heidelberg (2013)
19. Jansson, J., Sung, W.-K.: Constructing the  $R^*$  consensus tree of two trees in sub-cubic time. *Algorithmica* 66(2), 329–345 (2013)
20. Lott, M., Spillner, A., Huber, K.T., Petri, A., Oxelman, B., Moulton, V.: Inferring polyploid phylogenies from multiply-labeled gene trees. *BMC Evolutionary Biology* 9, 216 (2009)
21. Margush, T., McMorris, F.R.: Consensus  $n$ -Trees. *Bulletin of Mathematical Biology* 43(2), 239–244 (1981)
22. McMorris, F.R., Powers, R.C.: A characterization of majority rule for hierarchies. *Journal of Classification* 25(2), 153–158 (2008)
23. Page, R.: COMPONENT, version 2.0. Software package, University of Glasgow, U.K. (1993)
24. Ronquist, F., Huelsenbeck, J.P.: MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19(12), 1572–1574 (2003)
25. Sokal, R.R., Rohlf, F.J.: Taxonomic congruence in the Leptopodomorpha re-examined. *Systematic Zoology* 30(3), 309–325 (1981)
26. Sukumaran, J., Holder, M.T.: DendroPy: A Python library for phylogenetic computing. *Bioinformatics* 26(12), 1569–1571 (2010)
27. Sung, W.-K.: *Algorithms in Bioinformatics: A Practical Introduction*. Chapman & Hall/CRC (2010)
28. Swofford, D.L.: PAUP\*, version 4.0. Software package. Sinauer Associates, Inc., Sunderland (2003)