Fast Algorithms for Inferring Evolutionary Trees

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Abstract

We present algorithms for the perfect phylogeny problem restricted to binary characters. The first algorithm is faster than a previous algorithm by Gusfield when the input matrix for the problem is sparse. Next, we present two online algorithms. For the first of these, the characters are given as input one at a time, while, for the second, the species are given as input one at a time. These two online algorithms can easily be combined into an algorithm that can process any sequence of additions and deletions of species and characters.

1 Introduction

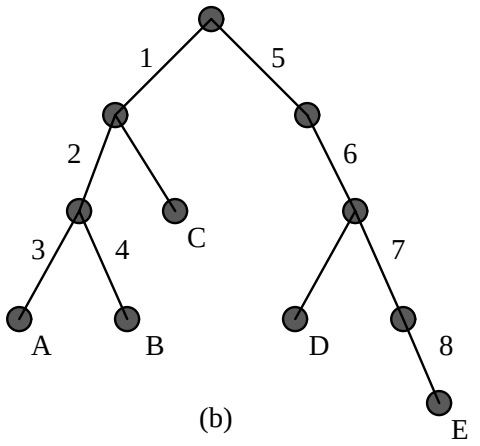
A fundamental problem in molecular biology is that of inferring the evolutionary history of a set of species, each of which is specified by the set of *traits* or *characters* that it exhibits [3, 4]. Each character can occur in a species in one of a fixed number of *states*. Information about evolutionary history can be conveniently represented by an evolutionary or *phylogenetic* tree, often referred to simply as a *phylogeny*. More precisely, a phylogeny for a set of species $\mathcal{S}$ is a rooted tree in which the leaves represent the species in $\mathcal{S}$, and the internal nodes represent hypothetical ancestral species. The species are usually described by an $n \times m$ matrix M, where $n = |\mathcal{S}|$ is the number of species, m is the number of characters, and M_{ij} is the state of the j^{th} character for the i^{th} species. A *perfect phylogeny* P, if it exists, is a phylogeny that assigns an m-vector of character states to each hypothesized ancestral species, and has the property that, for each state of each character, the set of nodes in P having that state is connected in P. Recently, this problem was shown to be NP-complete by Bodlaender et. al. [1].

When we restrict the characters to have only two states, M becomes a 0-1 matrix and an alternative but equivalent representation of P is a rooted tree where each species in $\mathcal{S}$ is attached to exactly one leaf of P, each character is associated with exactly one edge of P, and for any leaf w of P, the characters associated with the edges along the unique path from root to w exactly specify the characters of the species at leaf w. See Figure 1 for an example. We shall refer to this special case of perfect phylogeny problem as the *binary phylogeny (BP)* problem. For the biological assumptions and interpretation of this problem, see [5].

Gusfield [5] gave a time-optimal algorithm for solving BP which takes time linear in the size of the input matrix M. As he points out, the argument for the $\Omega(nm)$ lower

	1	2	3	4	5	6	7	8
A	1	1	1	0	0	0	0	0
B	1	1	0	1	0	0	0	0
C	1	0	0	0	0	0	0	0
D	0	0	0	0	1	1	0	0
E	0	0	0	0	1	1	1	1

(a)



(b)

Figure 1: (a) A matrix M and (b) its phylogenetic tree P.

bound considers a very unnatural matrix in which most of the species have most of the characters and M has $nm-2$ ones and only 2 zeroes. In general, however, M is not dense. For such instances, the following representation of the input may be more natural: For each character $i \in \{1, \cdots, m\}$, we are given a set C_i of all the species that exhibit that character; i.e., C_i is the set of species which have a 1 in column i of M. For convenience, we shall assume the existence of a universal set of species C_0 containing all n species. From now on, we shall refer to C_i as a character. We assume that all characters are nonempty. Our first result is a $O(C)$ algorithm for BP where $C = \sum_{i=1}^{m} |C_i|$. This is a significant improvement over the $O(nm)$ algorithm given in [5] for the case where M is sparse. Next, we give two online algorithms. The first one receives characters as input one at a time. We suggest two implementations of this algorithm and show that depending on the implementation, the running time of the algorithm for adding a character C_t is $O(|C_t| \log n)$ or $O(n)$. When invoked repeatedly for adding m characters, this yields a total running time of $O(C \log n)$ or $O(nm)$. The second online algorithm receives species as input one at a time. Similar implementations as those of the previous algorithm result in running time of $O(|I(S_t)| \log m)$ or $O(m)$ where S_t is the species being added and $|I(S_t)|$ is the number of ones in the row for S_t in M. This leads to a total running time of $O(C \log m)$ or $O(nm)$ for adding n species. Since, as pointed out in Sections 3 and 4, online deletion of characters and species from a given phylogeny can also be done quickly, we have a complete set of primitives for maintaining a phylogeny under any stream of additions and deletions of characters and species.

2 An algorithm for BP

Let $\mathcal{C} = \{C_0, \cdots, C_m\}$ be a set of characters. Gusfield's algorithm for BP and ours are based on the following fundamental result.

Lemma 1 *[2] $\mathcal{C}$ has a perfect phylogenetic tree P iff for every pair of characters C_i, C_j, either $C_i \cap C_j = \emptyset$ or one contains the other.*

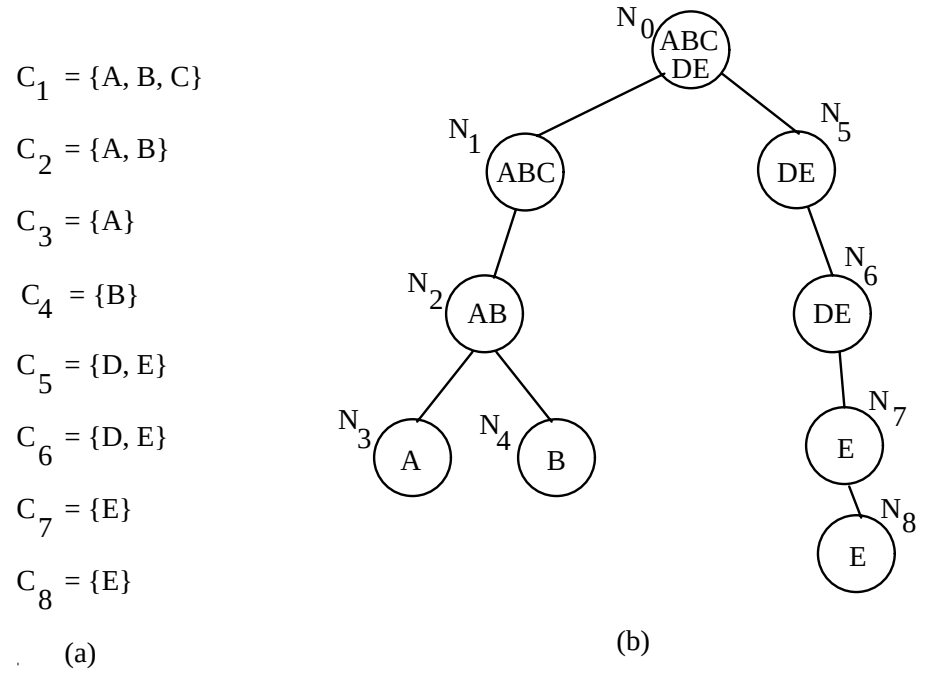


Figure 2: (a) Characters $C_1, \cdots, C_8$ and (b) their character tree T.

A set of characters $\mathcal{C}$ satifying the conditions of this lemma shall be said to be *compatible*.

Our approach is based on constructing a *character tree (CT)* T for $\mathcal{C}$. T is a rooted tree with the following properties:

(C1) $V(T) = \{N_0, \cdots, N_m\}$ where N_i is the node in T for character $C_i \in \mathcal{C}$. N_0 is the root of T.

(C2) For every $N_r \in V(T)$, if N_r has a parent N_p, then $C_r \subseteq C_p$.

(C3) For every $N_r \in V(T)$, $C_r \cap C_s = \emptyset$, for each sibling N_s of N_r.

By the above lemma, it is clear that $\mathcal{C}$ has a phylogenetic tree P iff it has a character tree. Given a character tree T for $\mathcal{C}$, we can easily construct a phylogenetic tree P for $\mathcal{C}$ as follows. First, for each $r \in \{1, \cdots, m\}$, label the edge between N_r and N_p by r, where N_p is the parent of N_r. Next, consider each N_i in turn. Let N_i be the parent of $N_{i_1}, \cdots, N_{i_r}$, and let $C_R = \cup_{j=1}^{r} C_{i_j}$. If $C_i - C_R = \emptyset$, do nothing. Otherwise, proceed as follows. If N_i is a leaf and $|C_i| = 1$, label N_i with the single species $x \in C_i$. Else, create a child of N_i for each $x \in C_i - C_R$ and label it by x.

Figure 2 shows the characters and the character tree for the example in Figure 1. From now on, we concentrate on constructing T. Algorithm PHYLOGENY, which is described below, creates T (if it exists) from the top down, inserting characters in nonincreasing order of cardinality. Each node has a list of links that point to the children of the node in T. PHYLOGENY also uses an array $A[1..n]$ where $A[i]$ stores the name of the (unique)

lowest node in T (constructed so far) containing species i. (Node a is *lower* than node b if the length of the path between a and the root is greater than the length of the path between b and the root.)

Algorithm PHYLOGENY

Step 1. Sort $C_0, \cdots, C_m$ by nonincreasing cardinality. From now on, we assume without loss of generality that $|C_0| \geq |C_1| \geq \cdots \geq |C_m|$. Create a node N_i for each character C_i and initialize all $A[i]$'s to N_0.

Step 2.

for $i = 1$ to m **do**
begin
  Pick a species $x \in C_i$; let $A[x] = N_l$
  for every $y \in C_i$ **do**
    if $A[y] \neq A[x]$ **then return** FAILURE
      else $A[y] \leftarrow N_i$
  Add a link from N_l to N_i
end

Step 1 can be carried out in $O(n + m + C)$ time by using radix sort with n buckets since for all i, $|C_i| \leq n$. In Step 2, we look at each C_i once and we look at each species in C_i at most once. Thus, Step 2 takes $O(C)$ time. The remaining bookkeeping can also be done in $O(C)$ time. Therefore, the running time of PHYLOGENY is $O(C)$, since usually $n \ll m$ and $m \leq C$.

Lemma 2 *If* PHYLOGENY *returns* FAILURE*, then* $\mathcal{C}$ *has no character tree.*

Proof: Suppose FAILURE occurs when C_i is being considered and we find that $A[y] \neq A[x]$. Let $A[x] = N_j$. Then $C_i \cap C_j \neq \emptyset$ since $x \in C_i \cap C_j$. Since C_j was considered before C_i, $|C_j| \geq |C_i|$. By Lemma 1, $\mathcal{C}$ has no character tree unless $C_j \supseteq C_i$.

Suppose $C_j \supseteq C_i$. We shall show that in this case there exists a C_k such that C_i and C_k violate Lemma 1. Since $A[y] \neq N_j$ and $y \in C_j$, we must have $A[y] = N_k$ where $j < k < i$. Now, $C_i \cap C_k \neq \emptyset$ because $y \in C_i \cap C_k$. Since $A[x] = N_j$ and $k > j$, $x \notin C_k$. Therefore, $x \in C_i$, $x \notin C_k$ and $C_k \not\supseteq C_i$. Since $|C_i| \leq |C_k|$, $C_i \not\supset C_k$ (we use $\subset$ and $\supset$ to denote proper inclusion). Therefore, C_i and C_k violate Lemma 1 and $\mathcal{C}$ has no character tree. □

Lemma 3 *If* PHYLOGENY *succeeds, then the tree constructed is a character tree for* $\mathcal{C}$*.*

Proof: Since we assume that all characters are nonempty, at the successful termination of PHYLOGENY, all the nodes will be in the constructed tree, say T. Hence T satisfies (C1). We show that conditions (C2) and (C3) are maintained after each iteration of the loop. Initially, these conditions are trivially true. Suppose they hold up to the $(r-1)^{th}$ iteration of the loop where $r > 0$. In the r^{th} iteration, we consider C_r. We argue that conditions (C2) and (C3) hold after the completion of this iteration.

Suppose N_p becomes the parent of N_r and $C_r \not\subseteq C_p$. Then there exists a $y \in C_r$ such that $y \notin C_p$. Thus, $A[y] \neq N_p$. Since N_p is the parent of N_r, the first species x picked

from C_r has $A[x] = N_p$. Therefore, $A[y] \neq A[x]$ and PHYLOGENY would return FAILURE. Hence $C_r \subseteq C_p$ and (C2) is satisfied.

If N_r has no siblings, then (C3) trivially holds true. Suppose N_r has siblings and their parent is N_p. Let x be the first species picked from C_r. Since N_p is the parent of N_r, we have $A[x] = N_p$. Let N_s be a sibling of N_r such that $C_r \cap C_s \neq \emptyset$ and let $y \in C_r \cap C_s$. Then $A[y]$ is either N_s or one of the descendants of N_s, but not N_p. Therefore, $A[y] \neq A[x]$ and PHYLOGENY would return FAILURE. Hence $C_r \cap C_s = \emptyset$ and (C3) is satisfied. □

3 An online algorithm for characters

It may sometimes be necessary to update an existing phylogeny or test if a newly introduced character is compatible with the current set of characters. In this section we consider an online algorithm for characters which answers the update and compatibility questions. Note that given a compatible set of characters $\mathcal{C}$, a CT R for $\mathcal{C}$, and a character C_t, the character set $\mathcal{C}' = \mathcal{C} - \{C_t\}$ is also compatible and a CT R' for $\mathcal{C}'$ can easily be constructed from R in $O(|C_t|)$ time. For this reason, in the remainder of this section, we concentrate on the problem of adding new characters.

In the online version for characters, characters arrive one at a time. Without loss of generality, we assume that characters are indexed $C_1, C_2, \cdots$, according to their order of arrival. As before, we stipulate the existence of a character C_0 which contains all n species and that all characters are nonempty. The online binary phylogeny problem is as follows: Given a compatible set of characters $\mathcal{C}_{t-1} = \{C_0, C_1, \cdots, C_{t-1}\}$ a character tree R_{t-1} for $\mathcal{C}_{t-1}$, and a character C_t, determine whether or not $\mathcal{C}_t = \mathcal{C}_{t-1} \cup \{C_t\}$ is a compatible set of characters and, if so, construct a character tree R_t for $\mathcal{C}_t$.

For convenience, we will work with a compact version of the character tree, which we shall refer to as a *compact character tree (CCT)*. It is equivalent to a character tree but renders itself more easily to online modifications by identifying nodes with identical characters as a single node. Formally, a CCT for a compatible set of characters $\mathcal{C} = \{C_0, \cdots, C_m\}$ is a tree R with vertex set $V(R) = \{N_0, N_{j_1}, \cdots, N_{j_l}\}$, where $\{j_1, \cdots, j_l\} \subseteq \{1, \cdots, m\}$, together with a labeling function *label* that maps every node in the tree to a subset of $\{1, \cdots, m\}$. R and *label* must satisfy the following properties:

(D1) N_0 is the root for R. (C_0 has all n species.)

(D2) For every $N_t \in V(R)$, if N_t has a parent N_p, then $C_t \subset C_p$.

(D3) For every $N_t \in V(R)$, $C_t \cap C_s = \emptyset$, for each sibling N_s of N_t.

(D4) For every $N_j \in V(R)$, $label(N_j) = \{i : C_i = C_j\}$.

(D5) $\cup\{label(N_j) : N_j \in V(R)\} = \{0, 1, \cdots, m\}$.

Figure 3 shows a CCT for the example in Figure 2. We have the following incremental version of Lemma 1, whose proof is omitted.

Lemma 4 *Suppose $\mathcal{C} = \{C_0, \cdots, C_{t-1}\}$ has a CCT R and C_t is the next character. Then $\mathcal{C} \cup \{C_t\}$ has a CCT R' iff either*

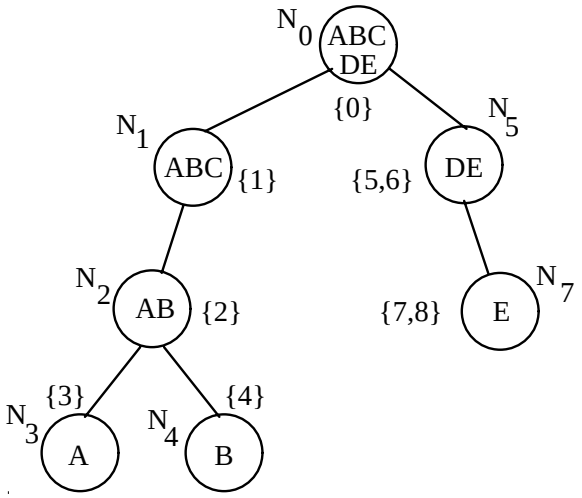


Figure 3: Compact character tree R for T in Figure 2

(E1) $C_t = C_p$ *for some* $C_p \in \mathcal{C}$, *or*

(E2) *There exists* $C_p \in \mathcal{C}$ *such that* $C_t \subset C_p$ *and for each child* N_r *of* N_p *in* R, $C_t \cap C_r = \emptyset$ *or* $C_t \supset C_r$.

Note that all characters C_p which satisfy (E2) will be equal and therefore, by (D4) they will be contained in the label set of a unique node in R. Furthermore, if $\mathcal{C} \cup \{C_t\}$ has a CCT R', then it can be obtained from R by carrying out the following transformation:

- If (E1) is satisfied, then add t to $label(N_p)$.
- If (E2) is satisfied, then create a node N_t, assign $label(N_t) = \{t\}$, and make N_p the parent of N_t. The children of N_t are those children N_r of N_p, if any, such that $C_t \supset C_r$.

This transformation is carried out by algorithm ONLINE-PHYLOGENY(R, C_t) given below which assumes that R is not empty (i.e., contains at least the root node N_0) and $C_t \neq \emptyset$. Because of the online requirement, the nodes of the tree will have to carry more information to facilitate fast processing of new characters. Specifically, each node $N_i \in V(R)$ stores
(i) the set C_i, denoted by $set(N_i)$,
(ii) $|C_i|$, the cardinality of C_i,
(iii) $parent(N_i)$, a pointer to the parent of N_i,
(iv) $label(N_i)$, the label set of N_i,
(v) list of pointers to its children, and
(vi) for every $x \in C_i$, a variable $H_i[x]$. $H_i[x]$ is a pointer to the child of N_i whose character contains the species x. If none of these contain x, then $H_i[x]$ is nil.

Algorithm ONLINE-PHYLOGENY(R, C_t)

```
    begin
        R' ← R
        Let v ← A[l] where l ∈ C_t and ∀i ∈ C_t, |set(A[l])| ≥ |set(A[i])|
        while |C_t| > |set(v)| do
            v ← parent(v)
        Let v = N_p                                          /* |C_t| ≤ |C_p| */
(⋆)     if C_t ⊈ C_p
(F1)        then return FAILURE
            else
                if |C_t| = |C_p|                             /* C_t is a duplicate of C_p */
(S1)                then Add t to label(N_p); return R'
                    else begin                               /* Now C_t ⊂ C_p */
                        create a new child N_t for N_p
                        label(N_t) ← {t}; parent(N_t) ← N_p
                        for every x ∈ C_t do begin
                            H_t[x] ← H_p[x]; H_p[x] ← N_t
                            if H_t[x] = nil
                                then A[x] ← N_t
                                else begin
                                    Let H_t[x] = N_r
                                    if parent(N_r) = N_p
(⋆⋆)                                    then if C_r ⊂ C_t
                                                then begin
                                                    Add a link from N_t to N_r
                                                    Remove the link from N_p to N_r
                                                    parent(N_r) ← N_t
                                                end
(F2)                                            else return FAILURE
                                end
                        endfor
(S2)                    return R'
                    end
    end
```

Lemma 5 *If* ONLINE-PHYLOGENY(R, C_t) *returns FAILURE, then* $\mathcal{C} \cup \{C_t\}$ *has no CCT.*

Proof: Suppose FAILURE occurs at (F1) when $|C_t| \leq |C_p|$ but $C_t \not\subseteq C_p$. Then neither one of C_t, C_p contains the other. Since N_p is an ancestor of $A[l]$, $l \in C_p \cap C_t$. Therefore, $C_t \cap C_p \neq \emptyset$ and C_t, C_p violate Lemma 1; thus, $\mathcal{C} \cup \{C_t\}$ has no CCT.

Suppose FAILURE occurs at (F2). Then $C_t \subset C_p$, but there exists $x \in C_t$ such that $H_t[x] = N_r \neq nil$, N_r is a child of N_p, and $C_r \not\subset C_t$. We first show that the node N_p found after the **while** loop is the only candidate for becoming the parent of N_t. Since l must be in the character set of the parent of N_t and $A[l]$ is the lowest node in R containing l, the parent of N_t lies on the path from $A[l]$ to the root of R. No node on the path from $A[l]$ to N_p can be the parent of N_t since the cardinality of its character set is smaller than $|C_t|$.

The nodes on the path from N_p to the root of R are not candidates for being a parent of N_t since they have a child which is neither disjoint from nor a subset of C_t. Therefore, N_p is the only candidate for becoming parent of N_t. Now, since $N_r = H_t[x] \neq nil$, $x \in C_r \cap C_t$. Hence, if $C_r \not\subset C_t$, (E2) is violated and $\mathcal{C} \cup \{C_t\}$ has no CCT. □

Lemma 6 *If* ONLINE-PHYLOGENY(R, C_t) *succeeds, then the tree R' constructed is a CCT for $\mathcal{C} \cup \{C_t\}$.*

Proof: If R' is returned at (S1), then there exists a $C_p \in \mathcal{C}$ such that $C_p = C_t$. In this case, the algorithm modifies R by adding label t to $label(N_p)$ in accordance with (D4). Since R satisfies (D1)-(D5), R' will also satisfy these conditions.

If R' is returned at (S2), then there is no $C_p \in \mathcal{C}$ such that $C_p = C_t$. In this case, the algorithm adds a new node N_t to R. N_t is made a child of a node N_p such that $C_t \subset C_p$ and made the parent of zero or more nodes N_r such that N_r is a child of N_p in R and $C_r \subset C_t$. Therefore, by (E2) R' is a CCT if C_t is disjoint from all C_r such that N_r is a child of N_p and $C_r \not\subset C_t$. Now if $x \in C_r \cap C_t$, then $x \in set(H_t[x]) \cap C_r$. Since $H_t[x]$ was a sibling of N_r in R, we have a contradiction as R satisfies (D3). □

Running time of ONLINE-PHYLOGENY(R, C_t): The time taken for finding the initial node v is $O(|C_t|)$ since each node N_i stores $|C_i|$. The number of iterations of the **while** loop is at most $|C_t|$ since R is a CCT and by (D2), $|set(parent(v))| \geq |set(v)| + 1$. The only costly operation in the algorithm is checking for set containment in $(\star)$ and $(\star\star)$. Clearly, $(\star)$ is carried out just once. For $(\star\star)$, we have the following. Let $N_{j_1}, \cdots, N_{j_k}$ be the children of N_t. Note that $\sum_{i=1}^{k} |C_{j_i}| \leq |C_t|$. For each child N_r of N_t, the operation $C_r \subset C_t$ is carried out precisely once when $parent(N_r)$ is set to N_t and therefore, for any other $x \in N_t \cap N_r$, the test for $parent(N_r) = N_p$ fails. We shall now present two implementations for carrying out the subset checking and analyze the running time for each case.

Sets as binary search trees: Each node N_i stores the species in C_i as a binary search tree S_i. The time required for checking whether $C_t \subseteq C_p$ is at most $O(|C_t| \log |C_p|)$ since for each element $x \in C_t$, we need to check whether x is in S_p which requires $O(\log |C_p|)$ time. Therefore, algorithm ONLINE-PHYLOGENY(R, C_t) takes $O(|C_t| \log |C_p|)$ time and by invoking it repeatedly, the phylogenetic tree can be found in $O(C \log n)$ time.

Sets as arrays: Each node N_i contains an array S_i of length n where $S_i[x] = 1$ if $x \in C_i$ and $S_i[x] = 0$ otherwise. S_i can be initialized in $O(n)$ time. The node also stores species in C_i as a linked list L_i. The time required to check whether $C_t \subseteq C_p$ is $O(|C_t|)$, since we need to examine each $x \in L_t$ exactly once, to check whether $S_p[x] = 1$. Therefore, algorithm ONLINE-PHYLOGENY(R, C_t) has a running time of $O(n)$ and the array implementation will have a total running time of $O(nm)$ for finding the phylogenetic tree.

4 An online algorithm for species

We now consider what, in a sense, is a dual version of the problem we studied in Section 3, namely, to dynamically maintain a CCT under a sequence of additions and deletions of

species. A species S is represented by the set $I(S)$ of the indices of the characters exhibited by S. Given a set $\mathcal{S}$ of species described in this way, there is a corresponding set $\mathcal{C}$ of characters, where each $C_i \in \mathcal{C}$ is given by $C_i = \{S \in \mathcal{S} : i \in I(S)\}$. We shall say that S is *compatible* if the associated set of characters $\mathcal{C}$ is compatible. As before, we shall assume that every species exhibits character C_0; i.e., $0 \in I(S)$ for all $S \in \mathcal{S}$.

Suppose we have a compatible set of species $\mathcal{S} = \{S_1, S_2, \cdots, S_{t-1}\}$ and a CCT R for $\mathcal{S}$. Clearly, for any $S_i \in \mathcal{S}$, the set of species $\mathcal{S}' = \mathcal{S} - \{S_i\}$ is compatible. Constructing a CCT R' for $\mathcal{S}'$ simply requires removing S_i from each node $N_j \in R$ such that $S_i \in C_j$. All of these nodes must lie on a single path in R. The removal of S_i may render identical two nodes which were formerly distinct sets C_j and C_k which differed only in S_i. Also, some set C_j may become empty and thus, N_j may have to be deleted from R. The key to updating R efficiently therefore, lies in representing the nodes and their associated sets properly. For example, if sets are represented as boolean arrays of length n, removal of a species S_i takes $O(1)$ time per set C_j such that $j \in I(S_i)$, for a total of $O(|I(S_i)|)$ time. Using a binary search tree representation of sets, removal of S_i from C_j when $j \in I(S_i)$ takes $O(\log n)$ time, for a total of $O(|I(S_i)| \cdot \log n)$ time per deletion. All other adjustments to R' can be done in $O(|I(S_i)|)$ time. For brevity, we shall leave the details to the reader and turn our attention to the problem of adding a species to $\mathcal{S}$.

Suppose we wish to determine whether $\mathcal{S}' = \mathcal{S} \cup \{S_t\}$ is compatible. Let $I(S_t) = \{0, i_1, i_2, \cdots, i_k\}$ be the indices of the characters of the new species S_t and R be the given tree; i.e., S_t should be added to each of the characters in $\{C_0, C_{i_1}, C_{i_2}, \cdots, C_{i_k}\}$. Our algorithm is based on the following result.

Lemma 7 *Suppose $\mathcal{S} = \{S_1, S_2, \cdots, S_{t-1}\}$ has a CCT R and S_t is the next species with $I(S_t) = \{0, i_1, \cdots, i_k\}$. Let $I_{old} = I(S_t) \cap I(\mathcal{S})$ where $I(\mathcal{S}) = \cup_{S_i \in \mathcal{S}} I(S_i)$. Then $\mathcal{S} \cup \{S_t\}$ is a compatible set of species iff there exists a path P in R from the root to some node $N_l \in V(R)$ such that both of the following conditions hold.*

(P1) $I_{old} \subseteq \cup\{label(N_i) : N_i \in P\}$.

(P2) $label(N_l) \cap I(S_t) \neq \emptyset$ *and for each* $N_i \in P - N_l$, $label(N_i) \subseteq I_{old}$.

Proof: We shall first argue that if there is no path P satisfying (P1) and (P2), then $\mathcal{S} \cup \{S_t\}$ is incompatible. Let P' be a longest path satisfying (P2). Note that there always exists such a path P' since $0 \in I(S_t) \cap label(N_0)$ where N_0 is the root of R. Since P' does not satisfy (P1) and every $i \in I(\mathcal{S})$ is present in the label set of exactly one node in R, there exist $N_j \in V(R)$ such that $N_j \notin P'$ and $label(N_j) \cap I(S_t) \neq \emptyset$. Suppose N_j is the highest such node. We now have following cases to consider:

Case 1: Suppose $parent(N_j) \in P'$ and there exists a sibling N_k of N_j such that $N_k \in P'$. By definition, $C_j \cap C_k = \emptyset$. Since $label(N_j) \cap I(S_t) \neq \emptyset$ and $label(N_k) \cap I(S_t) \neq \emptyset$, S_t must be added to both C_j and C_k. Therefore, $C_j \cup \{S_t\}$ and $C_k \cup \{S_t\}$ violate Lemma 1.

Case 2: Suppose $parent(N_j) = N_p \in P'$ and N_j has no sibling that lies on P'. Since P' is of maximum length and $N_j \notin P'$, $label(N_p) \not\subseteq I_{old}$ and $label(N_p) \cap I_{old} \neq \emptyset$. By definition, $C_j \subset C_p$. Let $f \in label(N_p) - I_{old}$. Since $f \notin I(S_t)$ and $j \in I(S_t)$, S_t gets added to C_j but not to C_f. Therefore, $C_j \cup \{S_t\}$ and C_f violate Lemma 1.

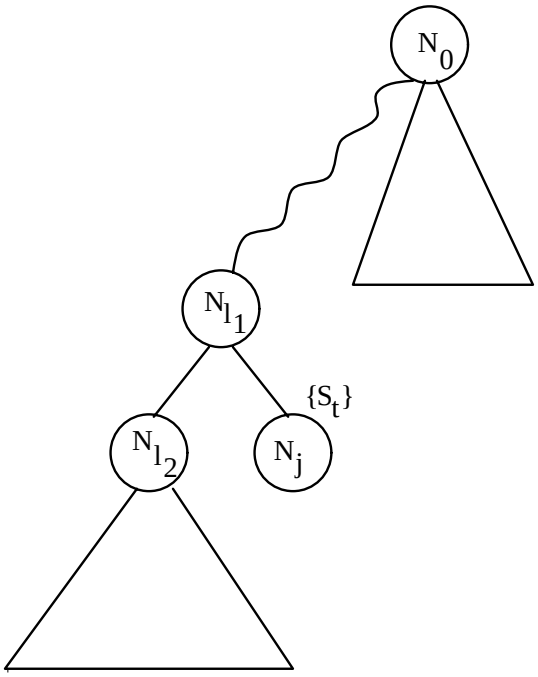


Figure 4: Dividing N_l into N_{l_1} and N_{l_2} and adding N_j

Case 3: Suppose $parent(N_j) = N_p \notin P'$. Then $label(N_p) \cap I(S_t) = \emptyset$ and S_t must be added to C_j but not to C_p. But then, $C_j \cup \{S_t\}$ and C_p violate Lemma 1.

In all cases, $\mathcal{S} \cup \{S_t\}$ is incompatible.

Now, suppose there exists a path P satisfying (P1) and (P2). We shall show that, in this case, we can build a CCT R' for $\mathcal{S}' = \mathcal{S} \cup \{S_t\}$ and hence, that $\mathcal{S}'$ is compatible. As before, let N_l be the lowest node in P.

First, let $J_1 = label(N_l) \cap I(S_t)$ and $J_2 = label(N_l) - J_1$. If $J_2 = \emptyset$, then add S_t to every $N_i \in P$. Otherwise, split N_l into two nodes as shown in Figure 4. The top one will be N_{l_1}, where l_1 is any element of J_1 and it will have $label(N_{l_1}) = J_1$. The other node will be N_{l_2}, where l_2 is any element of J_2 and it will have $label(N_{l_2}) = J_2$. Next, if $I_{old} \neq I(S_t)$, then choose any $j \in I(S_t) - I_{old}$ and create a new node N_j, which will be a child of N_{l_1}. Define $label(N_j) = I(S_t) - I_{old}$ and $set(N_j) = \{S_t\}$. Finally, S_t is added to N_{l_1} and to every $N_i \in P - N_l$. It is easy to verify that the resulting tree satisfies (D1)-(D5). □

An algorithm for adding a species to a compatible set of species immediately follows from the proof of the previous lemma. Since there can be only one path P satisfying the conditions of the above lemma, we can find it as follows: First, we find a node $N_l \in V(R)$ such that $label(N_l) \cap I(S_t) \neq \emptyset$ and $|C_l|$ is as small as possible. N_l will be the candidate for the lowest node in the path P. Next, we go up the tree from N_l, testing for each node N_i that we encounter whether $label(N_i) \subseteq I_{old}$. If this does not hold, then we return FAILURE. Otherwise, we test whether the union of the labels we encountered contains I_{old} (note that this can actually be done as we are going up the tree). If not, then return

FAILURE. Otherwise, the path P we have found satisfies the conditions of Lemma 7 and we modify the tree as specified in the proof of that lemma.

The lowest node N_l as required above can be efficiently found by keeping an array $B[1..m]$ where $B[i]$ is a pointer to the node $N_j \in V(R)$ such that $i \in label(N_j)$. Most of the work done by the algorithm we have sketched involves testing for a given $N_i \in V(R)$ whether $label(N_i) \subseteq I_{old}$. The only significant problem is the representation of labels so that this test can be done efficiently. As done for $set(N_i)$ in Section 3, we can implement $label(N_i)$ as either a boolean array of length m or as a binary search tree. The array implementation leads to a $O(m)$ running time per update and to a $O(nm)$ algorithm for adding n species. The binary search tree implementation leads to a $O(|I(S_t)| \cdot \log m)$ running time per update and to a $O(C \log m)$ running time algorithm for adding n species.

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