

A sharp lower bound for the number of phylogenetic trees displayed by a tree-child network

Dedicated to Andreas Dress in appreciation of his contributions to the phylogenetics community

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Abstract

A normal (phylogenetic) network with k reticulations displays 2^k phylogenetic trees. In this paper, we establish an analogous result for tree-child (phylogenetic) networks with no underlying 3-cycles. In particular, we show that a tree-child network with $k \geq 2$ reticulations and no underlying 3-cycles displays at least $2^{k/2}$ phylogenetic trees if k is even and at least $\frac{3}{2\sqrt{2}}2^{k/2}$ if k is odd. Moreover, we show that these bounds are sharp and characterise the tree-child networks that attain these bounds.

Keywords: phylogenetic tree, phylogenetic network, tree-child network, displayed tree

1 Introduction

Understanding the evolutionary history of a collection of present-day species is a central goal in biology, and rooted phylogenetic trees have traditionally been used for this purpose. However, evolution is not always strictly tree-like. Reticulate evolutionary events, such as hybridisation and lateral gene transfer, violate the assumptions underlying phylogenetic trees and instead require a more general model, (rooted) phylogenetic networks, to accurately represent evolutionary history.

Although species-level evolution can be non-tree-like, the evolution of individual genes is typically assumed to follow a tree-like pattern. As a result, a phylogenetic network is often viewed as

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an amalgamation of gene trees. This viewpoint leads to the notion of a rooted phylogenetic tree displayed (intuitively, embedded) by a phylogenetic network. Several algorithms have been implemented to compute a phylogenetic network that displays a given collection of rooted phylogenetic trees. These algorithms include the Autumn algorithm [7], TreeKnit [1], ALTS [16], FHyNCH [3], and PhyloFusion [17]. Relatedly, there has been substantial work on questions such as whether a phylogenetic network is (uniquely) determined by its displayed rooted phylogenetic trees [6, 9, 14], whether a particular rooted phylogenetic tree is displayed by a phylogenetic network [8, 13], and whether the number of rooted phylogenetic trees displayed by a given phylogenetic network can be computed in polynomial time [11]. It is the last of these questions that is the attention of this paper. In general, it is $\#P$ -complete to count the number of rooted binary phylogenetic trees displayed by a rooted binary phylogenetic network [11] and, despite some recent progress [2], it remains an open problem on whether this computational hardness extends to counting the number of rooted binary phylogenetic trees displayed by a tree-child network, a particular, but well studied, type of phylogenetic network. In this paper, we focus on obtaining a sharp lower bound for the number of rooted binary phylogenetic trees displayed by a tree-child network. We complete the introduction by stating the main result of the paper. Formal definitions are given in the next section.

Let $\mathcal{N}$ be a rooted binary phylogenetic network on X , and suppose that $\mathcal{N}$ has k reticulations. It is well-known that if $\mathcal{N}$ is normal, then $\mathcal{N}$ displays exactly 2^k rooted binary phylogenetic X -trees [13, 15]. (This is the maximum possible number of rooted binary phylogenetic trees displayed by $\mathcal{N}$.) However, if $\mathcal{N}$ is tree-child and we allow $\mathcal{N}$ to have underlying 3-cycles, then $\mathcal{N}$ could have many reticulations but still display only one rooted binary phylogenetic X -tree. What can we say if $\mathcal{N}$ is tree-child and has no underlying 3-cycles? The number of rooted binary phylogenetic trees displayed can still be strictly less than 2^k . But how much less? In this paper, we establish the following theorem, the main result of the paper. In the statement of the theorem, note that a rooted binary tree-child network with n leaves has at most $n - 1$ reticulations and an octopus is a particular type of tree-child network that we describe in the next section. Also, for a rooted binary phylogenetic network $\mathcal{N}$, we let $T(\mathcal{N})$ denote the set of (distinct) rooted binary phylogenetic trees displayed by $\mathcal{N}$.

Theorem 1.1. *Let $\mathcal{N}$ be a rooted binary tree-child network with n leaves, $0 \leq k \leq n - 1$ reticulations, and no underlying 3-cycles. If $k = 0$, then $|T(\mathcal{N})| = 1$, while if $k = 1$, then $|T(\mathcal{N})| = 2$. Furthermore, if $k \geq 2$, then*

- (i) $|T(\mathcal{N})| \geq 2^{k/2}$ if k is even, and
- (ii) $|T(\mathcal{N})| \geq \frac{3}{2\sqrt{2}} 2^{k/2}$ if k is odd.

Moreover, for all $k \geq 2$, we have that $|T(\mathcal{N})| = 2^{k/2}$ and k is even (respectively, $|T(\mathcal{N})| = \frac{3}{2\sqrt{2}} 2^{k/2}$ and k is odd) if and only if $\mathcal{N}$ is an octopus.

The paper is organised as follows. In the next section, we give some necessary definitions that clarify the terminology in the statement of Theorem 1.1 and are used throughout the rest of the paper. Section 3 establishes some preliminary lemmas, while Section 4 consists of the proof of Theorem 1.1.

2 Preliminaries

Throughout the paper X denotes a non-empty finite set.

Phylogenetic networks. A *rooted binary phylogenetic network on X* is a rooted acyclic directed graph with no parallel arcs such that

- (i) the (unique) root has in-degree zero and out-degree two,
- (ii) the set of vertices of out-degree zero is X ,
- (iii) all other vertices have either in-degree one and out-degree two, or in-degree two and out-degree one.

For technical reasons, if $|X| = 1$, then we allow $\mathcal{N}$ to consist of the single vertex in X . The set X is called the *leaf set* of $\mathcal{N}$. The vertices of in-degree one and out-degree two are *tree vertices*, while the vertices of in-degree two and out-degree one are *reticulations*. The arcs directed into a reticulation are called *reticulation arcs*; otherwise, an arc is a *tree arc*. If (u, v) is a reticulation arc in $\mathcal{N}$ and there is a directed path from u to v distinct from the path consisting of (u, v) , then (u, v) is a *shortcut*. A reticulation v is *normal* if neither reticulation arc directed into v is a shortcut. A *2-connected component* of $\mathcal{N}$ is a maximal (underlying) subgraph of $\mathcal{N}$ that is connected and cannot be disconnected by deleting exactly one of its vertices. We call a 2-connected component *trivial* if it consists of a single edge, and *non-trivial* otherwise. Furthermore, for brevity, we call an underlying 3-cycle of $\mathcal{N}$ a *3-cycle*. A *rooted binary phylogenetic X -tree $\mathcal{T}$* is a rooted binary phylogenetic network on X with no reticulations. Since all phylogenetic networks and phylogenetic trees in this paper are rooted and binary, we will refer to a rooted binary phylogenetic network and a rooted binary phylogenetic tree as a *phylogenetic network* and a *phylogenetic tree*, respectively.

A phylogenetic network $\mathcal{N}$ on X is *tree-child* if each non-leaf vertex is the parent of a tree vertex or a leaf. Equivalently, a phylogenetic network $\mathcal{N}$ is tree-child precisely if no tree vertex is the parent of two reticulations and no reticulation is the parent of another reticulation [12]. As an immediate consequence of the definition, if u is a vertex of a tree-child network $\mathcal{N}$, then there is a directed path from u to a leaf ℓ of $\mathcal{N}$ such that except for ℓ and possibly u , every vertex on the path is a tree vertex. We call such a path a *tree path (for u)*. As a result of this tree-path property, if $\mathcal{N}$ is a tree-child network with n leaves, then $\mathcal{N}$ has at most $n - 1$ reticulations, and this bound is sharp [4]. Also observe that if C is a 3-cycle of a tree-child network, then the arc set of C consists of two reticulation arcs directed into the same reticulation, one of which is a shortcut, and a tree arc. A tree-child network is *normal* if it has no shortcuts. To illustrate, in Fig. 1(i), $\mathcal{N}$ is a tree-child network, but it is not normal as the arc (u, v) is a shortcut. As with all other figures in the paper, arcs are directed down the page. It is directly because of shortcuts that the number of phylogenetic trees displayed by a tree-child network with k reticulations is not necessarily 2^k .

A lemma that we will frequently and freely use is the following [5].

Lemma 2.1. *Let $\mathcal{N}$ be a tree-child network with root ρ and let $e = (u, v)$ be a reticulation arc of $\mathcal{N}$. Then the phylogenetic network obtained from $\mathcal{N}$ by deleting e and either*

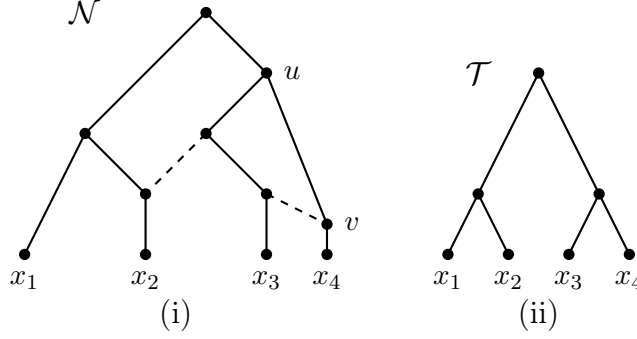


Fig. 1: (i) A tree-child network $\mathcal{N}$ on $X = \{x_1, x_2, x_3, x_4\}$ and (ii) a phylogenetic X -tree $\mathcal{T}$ displayed by $\mathcal{N}$.

- (i) suppressing the two resulting vertices of in-degree one and out-degree one if $u \neq \rho$, or
- (ii) suppressing the resulting vertex of in-degree one and out-degree one, and deleting u if $u = \rho$

is tree-child.

To ease reading, for a tree child network $\mathcal{N}$ and reticulation arc e of $\mathcal{N}$, we denote by $\mathcal{N} \setminus e$ the operation of deleting e and appropriately applying either (i) or (ii) of Lemma 2.1. We next describe two particular types of tree-child networks that are central to this paper.

Tight caterpillar ladders and octopuses. Let $\mathcal{N}$ be a tree-child network with vertex set $\{\ell_0, \ell_1, \ell_2, \ell_3\} \cup \{u_i, u'_i, v_i : i \in \{1, 2, 3\}\}$. We call $\mathcal{N}$ a 3-tight caterpillar ladder if the arc set of $\mathcal{N}$ is

$$\{(u'_3, u'_2), (u'_2, u_3), (u_3, u'_1), (u'_1, u_2), (u_2, u_1), (u_1, \ell_0)\} \cup \{(u'_i, v_i), (u_i, v_i), (v_i, \ell_i) : i \in \{1, 2, 3\}\}.$$

Note that $\{\ell_0, \ell_1, \ell_2, \ell_3\}$ is the leaf set of $\mathcal{N}$. The reticulation arcs (u_1, v_1) , (u_2, v_2) , (u'_1, v_1) , (u_3, v_3) , (u'_2, v_2) , and (u'_3, v_3) are the *rungs* of the 3-tight caterpillar ladder. Under this ordering, we refer to these rungs as the *i-th rung* so that, for example, (u_1, v_1) and (u'_3, v_3) are the *first* and *last* rungs of $\mathcal{N}$, respectively. Furthermore, a tree-child network is a 2-tight caterpillar ladder if it can be obtained from a 3-tight caterpillar by deleting, in this instance, u'_3 , v_3 , and ℓ_3 , and suppressing the resulting vertex of in-degree one and out-degree one. Here, for example, the *first* and *last* rungs are the arcs (u_1, v_1) and (u'_2, v_2) , respectively. For illustration, a 2-tight and a 3-tight caterpillar ladder are depicted in Fig. 2.

Let $k \in \{2, 3\}$. The *core* of a k -tight caterpillar ladder consists of its non-pendant arcs. Furthermore, let $\mathcal{N}$ be a k -tight caterpillar ladder and let $\mathcal{N}'$ be a tree-child network. We say that $\mathcal{N}$ is a k -tight caterpillar ladder of $\mathcal{N}'$ if, up to isomorphism, the core of $\mathcal{N}$ can be obtained from $\mathcal{N}'$ by deleting vertices and arcs.

Now let $\mathcal{N}$ be a tree-child network on X with n leaves and k reticulations, where $k \neq 1$. We call $\mathcal{N}$ an *octopus* if either k is even and every non-trivial 2-connected component of $\mathcal{N}$ is the core of a 2-tight caterpillar ladder, or k is odd, exactly one non-trivial 2-connected component of $\mathcal{N}$ is

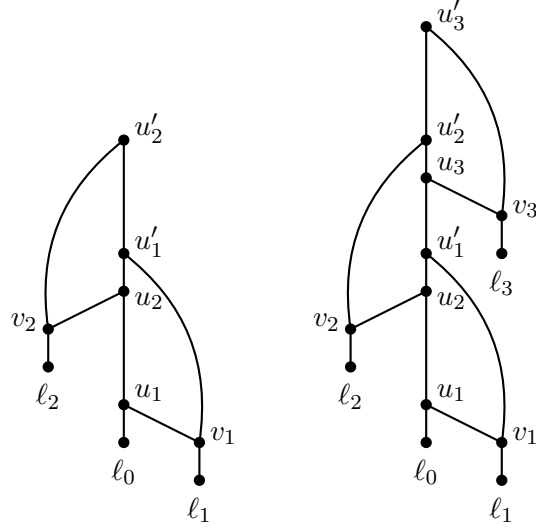


Fig. 2: A 2-tight (left) and a 3-tight (right) caterpillar ladder.

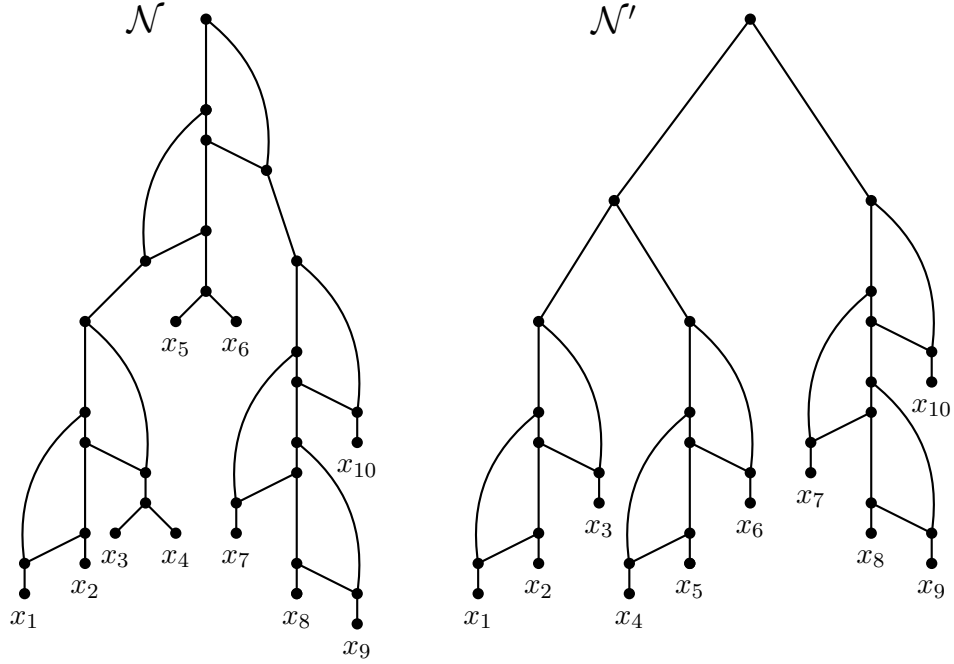


Fig. 3: Two octopuses $\mathcal{N}$ and $\mathcal{N}'$ with 10 leaves and 7 reticulations.

the core of a 3-tight caterpillar ladder, and every other non-trivial 2-connected component of $\mathcal{N}$ is the core of a 2-tight caterpillar ladder. To illustrate, in Fig. 3, $\mathcal{N}$ and $\mathcal{N}'$ are both octopuses with 10 leaves and 7 reticulations.

Displaying. Let $\mathcal{N}$ be a phylogenetic network on X and let $\mathcal{T}$ be a phylogenetic X -tree. We say that $\mathcal{N}$ *displays* $\mathcal{T}$ if a subdivision of $\mathcal{T}$ can be obtained from $\mathcal{N}$ by deleting vertices and arcs. Such a subdivision is an *embedding* of $\mathcal{T}$ in $\mathcal{N}$. If $\mathcal{N}$ is a tree-child network and $\mathcal{T}$ is a phylogenetic tree displayed by $\mathcal{N}$, then every embedding of $\mathcal{T}$ contains all of the tree arcs of $\mathcal{N}$ and, for each reticulation v , exactly one reticulation arc of $\mathcal{N}$ directed into v . Conversely, if F is a subset of the arcs of $\mathcal{N}$ that consists of all tree arcs and, for each reticulation v , exactly one reticulation arc directed into v , then F is an embedding of a phylogenetic tree displayed by $\mathcal{N}$ [12]. Thus to describe an embedding of $\mathcal{T}$ in $\mathcal{N}$ it suffices to specify the reticulation arcs of $\mathcal{N}$ in the embedding. Such arcs are *used* by $\mathcal{T}$. Also, as a reminder to the reader, we use $T(\mathcal{N})$ to denote the set of phylogenetic X -trees displayed by $\mathcal{N}$. To illustrate the notion of display, in Fig. 1, $\mathcal{N}$ displays $\mathcal{T}$, where an embedding of $\mathcal{T}$ in $\mathcal{N}$ is shown as solid arcs. Note that there is one other distinct embedding of $\mathcal{T}$ in $\mathcal{N}$.

Now let $\mathcal{N}$ be a phylogenetic network on X . An arc e of $\mathcal{N}$ is *non-essential* if, for every phylogenetic X -tree $\mathcal{T}$ in $T(\mathcal{N})$, there is an embedding of $\mathcal{T}$ in $\mathcal{N}$ that avoids e . The next lemma is a special case of a more general result established in [10].

Lemma 2.2. *Let $\mathcal{N}$ be a tree-child network with n leaves and k reticulations, where $k \in \{2, 3\}$, and let e be an arc of $\mathcal{N}$. Then e is non-essential if and only if e is either the first or last rung of a 2- or 3-tight caterpillar ladder of $\mathcal{N}$.*

Phylogenetic trees. Let $\mathcal{T}$ be a phylogenetic X -tree, and let X' be a subset of X . The minimal subtree of $\mathcal{T}$ connecting the elements in X' is denoted by $\mathcal{T}(X')$. Furthermore, the *restriction of $\mathcal{T}$ to X'* is the phylogenetic X' -tree obtained from $\mathcal{T}(X')$ by suppressing vertices of in-degree one and out-degree one. A subtree of $\mathcal{T}$ is *pendant* if it can be obtained by deleting an edge of $\mathcal{T}$, in which case the leaf set of this pendant subtree is a *cluster* of $\mathcal{T}$. Furthermore, two phylogenetic X -trees $\mathcal{T}_1$ and $\mathcal{T}_2$ are *isomorphic* if there is a map $\varphi : V(\mathcal{T}_1) \rightarrow V(\mathcal{T}_2)$ such that, for all $x \in X$, we have $\varphi(x) = x$ and, if (u, v) is an arc of $\mathcal{T}_1$, then $(\varphi(u), \varphi(v))$ is an arc of $\mathcal{T}_2$.

A *caterpillar* is a phylogenetic tree whose leaf set can be ordered $x_1, x_2, \dots, x_n$ so that x_1 and x_2 have the same parent and, for all $i \in \{3, 4, \dots, n\}$, the parent of x_{i-1} is a child of the parent of x_i . We denote such a caterpillar by $(x_1, x_2, \dots, x_n)$. A *double caterpillar* is a phylogenetic tree such that its maximal pendant subtrees are both caterpillars. If $(x_1, x_2, \dots, x_i)$ and $(y_1, y_2, \dots, y_j)$ are two such caterpillars, then we denote the double caterpillar by $\{(x_1, x_2, \dots, x_i), (y_1, y_2, \dots, y_j)\}$.

3 Some lemmas

In this section we establish some lemmas that will be used in the proof of Theorem 1.1. For the first lemma, recall that a tree-child network with n leaves has at most $n - 1$ reticulations. Let $n \geq 1$

and $0 \leq k \leq n - 1$ be two non-negative integers. For all n and k , set

$$t(n, k) = \begin{cases} 1, & \text{if } k = 0; \\ 2, & \text{if } k = 1; \\ 2^{k/2}, & \text{if } k \geq 2 \text{ and } k \text{ is even;} \\ \frac{3}{2\sqrt{2}}2^{k/2}, & \text{if } k \geq 3 \text{ and } k \text{ is odd.} \end{cases}$$

Observe that, for all n and k , the value $t(n, k)$ is the bound given in the statement of Theorem 1.1. The next lemma establishes some basic properties of the numbers $t(n, k)$. These properties are repeatedly used in the proof of Theorem 1.1.

Lemma 3.1. *The following identities hold:*

- (i) For all $n \geq 2$, we have $t(n, 1) = 2 \cdot t(n, 0)$ and, for all $n \geq 3$, we have $t(n, 2) = 2 \cdot t(n, 1)$.
- (ii) For all $n \geq 4$, we have $t(n, 3) = t(n, 2) + t(n, 0) < 2 \cdot t(n, 1) = t(n, 2) + t(n, 1)$.
- (iii) For all $n \geq 4$ and $2 \leq k \leq n - 2$, we have $t(n, k) < t(n, k + 1)$.
- (iv) For all $n \geq 4$ and $3 \leq k \leq n - 1$, we have $t(n, k) < 4 \cdot t(n, k - 3)$.
- (v) For all $n \geq 5$ and $4 \leq k \leq n - 1$,

$$t(n, k) = 2 \cdot t(n, k - 2) < t(n, k - 1) + t(n, k - 2).$$

- (vi) For all $n \geq 4$ and $3 \leq k \leq n - 1$, and k is odd,

$$t(n, k) = t(n, k - 1) + t(n, k - 3)$$

while, for all $n \geq 5$ and $4 \leq k \leq n - 1$, and k is even,

$$t(n, k) < t(n, k - 1) + t(n, k - 3).$$

Proof. The proof of (i) is trivial. For the proof of (ii), if $n \geq 4$, then

$$t(n, 3) = \frac{3}{2\sqrt{2}}2^{3/2} = 3 = t(n, 2) + t(n, 0) < 4 = 2 \cdot t(n, 1) = t(n, 2) + t(n, 1).$$

For the proof of (iii), if $n \geq 4$, $2 \leq k \leq n - 2$, and k is even, then

$$t(n, k) = 2^{k/2} < \frac{3}{2} \cdot 2^{k/2} = \frac{3}{2\sqrt{2}}2^{k/2} \cdot \sqrt{2} = \frac{3}{2\sqrt{2}}2^{(k+1)/2} = t(n, k + 1)$$

while if $n \geq 4$, $2 \leq k \leq n - 2$, and k is odd, then

$$t(n, k) = \frac{3}{2\sqrt{2}}2^{k/2} = 3 \cdot 2^{(k-3)/2} < 4 \cdot 2^{(k-3)/2} = 2^{(k+1)/2} = t(n, k + 1).$$

Now consider (iv). If $n \geq 4$ and $k = 3$, then $t(n, 3) = 3 < 4 = 4 \cdot t(n, 0)$ and, if $n \geq 5$ and $k = 4$, then $t(n, 4) = 4 < 8 = 4 \cdot t(n, 1)$, so we may assume that $n \geq 6$ and $5 \leq k \leq n - 1$. If k is odd, then

$$t(n, k) = \frac{3}{2\sqrt{2}}2^{k/2} = 3 \cdot 2^{(k-3)/2} < 4 \cdot 2^{(k-3)/2} < 4 \cdot t(n, k - 3),$$

while if k is even, then

$$t(n, k) = 2^{k/2} = 2 \cdot 2^{(k-2)/2} < 3 \cdot 2^{(k-2)/2} = 4 \cdot \frac{3}{2\sqrt{2}} 2^{(k-3)/2} = 4 \cdot t(n, k-3).$$

For the proof of (v), if $n \geq 5$, $4 \leq k \leq n-1$, and k is even, then, by (iii),

$$t(n, k) = 2^{k/2} = 2 \cdot 2^{(k-2)/2} = 2 \cdot t(n, k-2) < t(n, k-1) + t(n, k-2).$$

If $n \geq 5$, $4 \leq k \leq n-1$, and k is odd, then, by (iii),

$$t(n, k) = \frac{3}{2\sqrt{2}} 2^{k/2} = 2 \cdot \frac{3}{2\sqrt{2}} 2^{(k-2)/2} = 2 \cdot t(n, k-2) < t(n, k-1) + t(n, k-2).$$

Lastly, consider (vi). If $n \geq 4$ and $k = 3$, then

$$t(n, k-1) + t(n, k-3) = t(n, 2) + t(n, 0) = t(n, 3).$$

Furthermore, if $n \geq 6$, $3 \leq k \leq n-1$, and k is odd, then, as $k-1$ and $k-3$ are even,

$$\begin{aligned} t(n, k-1) + t(n, k-3) &= 2^{(k-1)/2} + 2^{(k-3)/2} = 2^{(k-3)/2} (2+1) \\ &= 3 \cdot 2^{(k-3)/2} = \frac{3}{2\sqrt{2}} 2^{k/2} = t(n, k). \end{aligned}$$

If $n \geq 5$, $4 \leq k \leq n-1$, and k is even, then, as $k-1$ and $k-3$ are odd,

$$\begin{aligned} t(n, k-1) + t(n, k-3) &= \frac{3}{2\sqrt{2}} 2^{(k-1)/2} + \frac{3}{2\sqrt{2}} 2^{(k-3)/2} = \frac{3}{2\sqrt{2}} 2^{(k-3)/2} (2+1) \\ &> \frac{2^3}{2\sqrt{2}} 2^{(k-3)/2} = 2^{k/2} = t(n, k). \end{aligned}$$

□

The next lemma establishes the number of distinct phylogenetic trees displayed by an octopus.

Lemma 3.2. *Let $\mathcal{N}$ be an octopus with n leaves and $k \neq 1$ reticulations. Then $|T(\mathcal{N})| = t(n, k)$.*

Proof. The proof is by induction on k . Evidently, if $k = 0$, then $|T(\mathcal{N})| = 1 = t(n, 0)$. Furthermore, if $k = 2$, then $\mathcal{N}$ contains precisely one non-trivial 2-connected component which is the core of a 2-tight caterpillar ladder and it is easy to verify that $|T(\mathcal{N})| = 2 = t(n, 2)$. Similarly, if $k = 3$, then $\mathcal{N}$ contains precisely one non-trivial 2-connected component which is the core of a 3-tight caterpillar ladder and $|T(\mathcal{N})| = 3 = t(n, 3)$. Thus the lemma holds for $k \in \{0, 2, 3\}$.

Now suppose that $k \geq 4$, in which case $n \geq 5$, and the lemma holds for all octopuses with at most $k-1$ reticulations. Let v be a reticulation of $\mathcal{N}$ with the property that all paths starting at v are tree paths, that is, there are no other reticulations among the descendants of v . As $\mathcal{N}$ is an octopus, v is a reticulation of either a 2-tight or 3-tight caterpillar ladder, say $\mathcal{N}'$, of $\mathcal{N}$.

Assume that $\mathcal{N}'$ is a 2-tight caterpillar ladder of $\mathcal{N}$. Let $\mathcal{N}_1$ be the tree-child network obtained from $\mathcal{N}$ by deleting the third and last rungs of $\mathcal{N}'$, and let $\mathcal{N}_2$ be the tree-child network obtained

from $\mathcal{N}$ by deleting the first and last rungs of $\mathcal{N}'$. Clearly, $\mathcal{N}_1$ and $\mathcal{N}_2$ are octopuses with n leaves and $k - 2$ reticulations. Moreover, observe that $T(\mathcal{N}_1) \cap T(\mathcal{N}_2)$ is empty and, if $\mathcal{T} \in T(\mathcal{N})$, then either $\mathcal{T} \in T(\mathcal{N}_1)$ or $\mathcal{T} \in T(\mathcal{N}_2)$. Thus, by induction and Lemma 3.1(v),

$$|T(\mathcal{N})| = |T(\mathcal{N}_1)| + |T(\mathcal{N}_2)| = t(n, k - 2) + t(n, k - 2) = t(n, k).$$

Now assume that $\mathcal{N}'$ is a 3-tight caterpillar ladder of $\mathcal{N}$, in which case, k is odd and so $k \geq 5$. Let $\mathcal{N}_1$, $\mathcal{N}_2$, and $\mathcal{N}_3$ be the octopuses on $k - 3$ reticulations obtained from $\mathcal{N}$ by deleting the third, fifth, and last rungs of $\mathcal{N}'$, the first, fifth, and last rungs of $\mathcal{N}'$, and the second, third, and last rungs of $\mathcal{N}'$, respectively. It is easily verified that $T(\mathcal{N}_i) \cap T(\mathcal{N}_j) = \emptyset$ for all distinct $i, j \in \{1, 2, 3\}$. Furthermore, if $\mathcal{T} \in T(\mathcal{N})$, then $\mathcal{T} \in T(\mathcal{N}_1) \cup T(\mathcal{N}_2) \cup T(\mathcal{N}_3)$. Therefore, as k is odd, it follows by induction that

$$\begin{aligned} |T(\mathcal{N})| &= |T(\mathcal{N}_1)| + |T(\mathcal{N}_2)| + |T(\mathcal{N}_3)| \\ &= t(n, k - 3) + t(n, k - 3) + t(n, k - 3) \\ &= 3 \cdot 2^{(k-3)/2} = \frac{3}{2\sqrt{2}} 2^{k/2} = t(n, k). \end{aligned}$$

This completes the proof of the lemma. $\square$

For the proof of Theorem 1.1, we need to understand what happens if we delete a reticulation arc of a tree-child network and create a 3-cycle. The next three lemmas consider tree-child networks and 3-cycles.

Lemma 3.3. *Let $\mathcal{N}$ be a tree-child network with no 3-cycles, and let e be a reticulation arc of $\mathcal{N}$. Suppose that $\mathcal{N} \setminus e$ has a 3-cycle with reticulation arcs f and f' . Then each of $\mathcal{N} \setminus \{e, f\}$ and $\mathcal{N} \setminus \{e, f'\}$ is tree-child and has no 3-cycles.*

Proof. Consider $\mathcal{N} \setminus e$ and denote the arcs of the 3-cycle of $\mathcal{N} \setminus e$ as $f = (u_1, v)$, $f' = (u_2, v)$, and $h = (u_1, u_2)$. In particular, v is a reticulation, and f is a shortcut of $\mathcal{N}$ and $\mathcal{N} \setminus e$. Note that $\mathcal{N}$ and $\mathcal{N} \setminus e$ contain the arcs f and f' , but $\mathcal{N}$ does not contain h . Instead, $\mathcal{N}$ contains two arcs, say $h_1 = (u_1, s)$ and $h_2 = (s, u_2)$, such that $e = (s, t)$ is the reticulation arc that is deleted to obtain $\mathcal{N} \setminus e$ from $\mathcal{N}$. We now argue that both $\mathcal{N} \setminus \{e, f\}$ and $\mathcal{N} \setminus \{e, f'\}$ are tree-child and have no 3-cycles.

First, consider $\mathcal{N} \setminus \{e, f\}$ and suppose that it contains a 3-cycle, say C . Then C contains the arc (p, u_2) , where p is the unique parent of u_1 in $\mathcal{N}$. The two remaining arcs of C are reticulation arcs, say (p, r) and (u_2, r) , where $r \neq v$ is a reticulation in $\mathcal{N} \setminus \{e, f\}$ and also in $\mathcal{N}$. Since there is also an arc (u_2, v) in $\mathcal{N}$ and v is a reticulation, this implies that both children of u_2 are reticulations, contradicting the fact that $\mathcal{N}$ is tree-child. Thus $\mathcal{N} \setminus \{e, f\}$ is tree-child and has no 3-cycle.

Next, consider $\mathcal{N} \setminus \{e, f'\}$ and suppose that it contains a 3-cycle, say C' . Then C' contains the arc (u_1, w) , where $w \neq v$ is a child of u_2 in $\mathcal{N}$. As $\mathcal{N}$ is tree-child, w is a tree vertex. Thus the two remaining arcs of C' are reticulation arcs incident with the same reticulation, say $r' \neq v$. But then (u_1, r') is an arc of C' and so, as r' is a reticulation of $\mathcal{N}$, the vertex u_1 is the parent of two reticulations in $\mathcal{N}$, a contradiction as $\mathcal{N}$ is tree-child. Therefore $\mathcal{N} \setminus \{e, f'\}$ is tree-child and has no 3-cycles, thereby completing the proof of the lemma. $\square$

Lemma 3.4. *Let $\mathcal{N}$ be a tree-child network with no 3-cycles, and let $e = (u, v)$ be a reticulation arc of $\mathcal{N}$ such that, amongst all reticulation arcs of $\mathcal{N}$, u has minimum distance to the root of $\mathcal{N}$. Then $\mathcal{N} \setminus e$ is tree-child and has no 3-cycles.*

Proof. If $\mathcal{N} \setminus e$ has a 3-cycle, then the parent p of u in $\mathcal{N}$ has a child that is a reticulation. But then p is closer to the root of $\mathcal{N}$ than u , a contradiction. Hence $\mathcal{N} \setminus e$ has no 3-cycles. $\square$

The last lemma in this section is a technical lemma that is used in the inductive proof of Theorem 1.1. Recall that a reticulation is normal if neither reticulation arc directed into it is a shortcut.

Lemma 3.5. *Let $\mathcal{N}$ be a tree-child network with n leaves, $k \geq 2$ reticulations, and no 3-cycles. Suppose that $\mathcal{N}$ has a normal reticulation and, for all tree-child networks $\mathcal{N}'$ with n leaves, $k' < k$ reticulations, and no 3-cycles, $|T(\mathcal{N}')| \geq t(n, k')$. Then $|T(\mathcal{N})| > t(n, k)$.*

Proof. Let v be a normal reticulation of $\mathcal{N}$, and let e_1 and e_2 denote the reticulation arcs directed into v . The proof is partitioned into three cases depending on whether zero, one, or two of $\mathcal{N} \setminus e_1$ and $\mathcal{N} \setminus e_2$ has a 3-cycle. We establish the lemma for when each of $\mathcal{N} \setminus e_1$ and $\mathcal{N} \setminus e_2$ has a 3-cycle. The other two cases are proved similarly, but are less complicated.

Let $e_1 = (u_1, v)$ and $e_2 = (u_2, v)$, and let m be a leaf at the end of a tree path starting at v . For each $i \in \{1, 2\}$, let w_i and w'_i denote the child of u_i that is not v and the parent of u_i , respectively. Since $\mathcal{N}$ is tree-child and each of $\mathcal{N} \setminus e_1$ and $\mathcal{N} \setminus e_2$ has a 3-cycle, for each i , the vertices w_i and w'_i are tree vertices and the parent of a reticulation v_i . For each i , let $f_i = (w_i, v_i)$ and $f'_i = (w'_i, v_i)$, and let m_i be a leaf at the end of a tree path starting at v_i . Furthermore, let ℓ_i be a leaf at the end of a tree path starting at w_i . Observe that ℓ_1, ℓ_2, m, m_1 , and m_2 are distinct as v is normal and neither e_1 nor e_2 is a shortcut.

Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses $\{e_2, f_1, f'_2\}$ or $\{e_2, f_1, f_2\}$, then $\mathcal{T}[\{\ell_1, \ell_2, m, m_1, m_2\}] \cong \{(\ell_1, m_1), (m, \ell_2, m_2)\}$ and $\mathcal{T}[\{\ell_1, \ell_2, m, m_1, m_2\}] \cong \{(\ell_1, m_1), (\ell_2, m_2, m)\}$, respectively. On the other hand, if $\mathcal{T}$ uses $\{e_1, f_2, f'_1\}$ or $\{e_1, f_2, f_1\}$, then $\mathcal{T}[\{\ell_1, \ell_2, m, m_1, m_2\}] \cong \{(\ell_1, m, m_1), (\ell_2, m_2)\}$ and $\mathcal{T}[\{\ell_1, \ell_2, m, m_1, m_2\}] \cong \{(\ell_1, m_1, m), (\ell_2, m_2)\}$, respectively. It now follows that

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus \{e_1, f'_1, f_2\})| + |T(\mathcal{N} \setminus \{e_1, f'_1, f'_2\})| + |T(\mathcal{N} \setminus \{e_2, f'_2, f_1\})| + |T(\mathcal{N} \setminus \{e_2, f'_2, f'_1\})|,$$

and so, by Lemmas 3.1(iv) and 3.3, and the assumption in the statement of the lemma,

$$|T(\mathcal{N})| \geq t(n, k-3) + t(n, k-3) + t(n, k-3) + t(n, k-3) > t(n, k).$$

This completes the proof of the lemma. $\square$

4 Proof of Theorem 1.1

The proof of Theorem 1.1 is inductive and relies on first showing that the theorem holds for all $k \in \{0, 1, 2, 3\}$, the base cases. The next lemma establishes this base case.

Lemma 4.1. *Let $\mathcal{N}$ be a tree-child network with n leaves, $k \in \{0, 1, 2, 3\}$ reticulations, and no 3-cycles. Then $|T(\mathcal{N})| = 1$ if $k = 0$, $|T(\mathcal{N})| = 2$ if $k = 1$, and*

$$|T(\mathcal{N})| \geq \begin{cases} 2, & \text{if } k = 2; \\ 3, & \text{if } k = 3. \end{cases}$$

Furthermore, if $|T(\mathcal{N})| = 2$ and $k = 2$ or $|T(\mathcal{N})| = 3$ and $k = 3$, then $\mathcal{N}$ is an octopus.

Proof. Evidently, if $k = 0$, then $|T(\mathcal{N})| = 1$. Furthermore, as $\mathcal{N}$ has no 3-cycles, if $k = 1$, then $|T(\mathcal{N})| = 2$, so the lemma holds for $k \in \{0, 1\}$. For the remainder of the proof, we may assume without loss of generality that, amongst all tree-child networks with n leaves, $k \in \{2, 3\}$ reticulations, and no 3-cycles, $|T(\mathcal{N})|$ is minimised, in which case, by Lemma 3.2, $|T(\mathcal{N})| \leq t(n, k)$.

First, consider when $k = 2$. Let $f = (u, v)$ be a reticulation arc of $\mathcal{N}$ such that, amongst all reticulation arcs of $\mathcal{N}$, the vertex u has minimum distance to the root of $\mathcal{N}$. By Lemma 3.4, $\mathcal{N} \setminus f$ is tree-child and has no 3-cycles. Therefore, as $\mathcal{N} \setminus f$ has exactly one reticulation, it follows by the previous base case that $|T(\mathcal{N} \setminus f)| = 2$. Furthermore, by Lemma 3.2, $|T(\mathcal{N})| \leq t(n, 2) = 2$, and so

$$|T(\mathcal{N})| = |T(\mathcal{N} \setminus f)| = 2.$$

Thus f is non-essential, and, by Lemma 2.2, f is the first or last rung of a 2-tight caterpillar ladder of $\mathcal{N}$ (in fact, by the choice of f , it is the last rung). As $k = 2$, this implies that $\mathcal{N}$ is an octopus, thereby completing the proof for when $k = 2$.

Now consider when $k = 3$. Again, let $f = (u, v)$ be a reticulation arc of $\mathcal{N}$ such that, amongst all reticulation arcs of $\mathcal{N}$, the vertex u has minimum distance to the root of $\mathcal{N}$. Lemma 3.4 implies that $\mathcal{N} \setminus f$ is tree-child and has no 3-cycles. Furthermore, as $\mathcal{N} \setminus f$ has exactly two reticulations, it follows by the previous base case that $|T(\mathcal{N} \setminus f)| \geq 2$. Additionally, by Lemma 3.2, $|T(\mathcal{N})| \leq t(n, 3) = 3$, and so $|T(\mathcal{N})| \in \{2, 3\}$.

First, suppose that $|T(\mathcal{N})| = 2$. Then $|T(\mathcal{N})| = |T(\mathcal{N} \setminus f)| = 2$, and so f is non-essential. By Lemma 2.2 and the choice of f , we have that f is the last rung of a 2-tight or 3-tight caterpillar ladder of $\mathcal{N}$. If f is the last rung of a 3-tight caterpillar ladder, then $\mathcal{N}$ is an octopus and $|T(\mathcal{N})| = 3$, a contradiction as $|T(\mathcal{N})| = 2$. Therefore f is the last rung of a 2-tight caterpillar ladder of $\mathcal{N}$ with reticulations, v_1 and v_2 say. Let v_3 denote the third reticulation in $\mathcal{N}$, and let g_1 and g_2 be the reticulation arcs of $\mathcal{N}$ directed into v_3 .

Assume that either $\mathcal{N} \setminus g_1$ or $\mathcal{N} \setminus g_2$ has no 3-cycle. Without loss of generality, assume $\mathcal{N} \setminus g_1$ has no 3-cycle. By the previous base case, $|T(\mathcal{N} \setminus g_1)| \geq 2$ and, by assumption, $|T(\mathcal{N})| = 2$, implying that $|T(\mathcal{N})| = |T(\mathcal{N} \setminus g_1)| = 2$, and so g_1 is non-essential. Therefore, by Lemma 2.2, g_1 is either the first or last rung of a 2-tight or 3-tight caterpillar ladder of $\mathcal{N}$. However, as $k = 3$ and $\mathcal{N}$ contains a 2-tight caterpillar ladder with reticulations v_1 and v_2 , and $v_3 \notin \{v_1, v_2\}$, this is not possible. Thus, for each $i \in \{1, 2\}$, the tree-child network $\mathcal{N} \setminus g_i$ has a 3-cycle. But neither 3-cycle involves v_1 nor v_2 as they are the reticulations of a 2-tight caterpillar ladder of $\mathcal{N}$, and so this is also not possible. In summary, we cannot have $|T(\mathcal{N})| = 2$, and so $|T(\mathcal{N})| = 3$. It remains to show that $\mathcal{N}$ is an octopus.

Suppose that $|T(\mathcal{N})| = 3$. By Lemma 3.4, $\mathcal{N} \setminus f$ is tree-child and has no 3-cycles. Furthermore, by the previous base case, $|T(\mathcal{N} \setminus f)| \geq 2$ and so, as $|T(\mathcal{N})| = 3$, we have $|T(\mathcal{N} \setminus f)| \in \{2, 3\}$. We now distinguish two cases depending on $|T(\mathcal{N} \setminus f)|$:

- (a) If $|T(\mathcal{N} \setminus f)| = |T(\mathcal{N})| = 3$, then f is non-essential and, by Lemma 2.2 and the choice of f , it is the last rung of a 2-tight or 3-tight caterpillar ladder of $\mathcal{N}$. If f is the last rung of a 3-tight caterpillar ladder of $\mathcal{N}$, then $\mathcal{N}$ is an octopus, and so we may assume that f is the last rung of a 2-tight caterpillar ladder of $\mathcal{N}$ with reticulations v_1 and v_2 , and core arcs

$$\{(u'_2, u'_1), (u'_1, u_2), (u_2, u_1), (u'_1, v_1), (u_1, v_1), (u'_2, v_2), (u_2, v_2)\}.$$

Note that $f = (u, v) = (u'_2, v_2)$. Let v_3 be the third reticulation of $\mathcal{N}$ and let $g_1 = (u_3, v_3)$ and $g_2 = (u'_3, v_3)$ denote the reticulation arcs of $\mathcal{N}$ directed into v_3 . For each $i \in \{1, 2, 3\}$, let m_i denote a leaf at the end of a tree path starting at v_i . Furthermore, let a, b , and c denote a leaf at the end of a tree path starting at u_1, u_3 , and u'_3 , respectively. Note that $m_1 \neq m_2 \neq m_3$, $a \neq m_1$, $a \neq m_2$, $b \neq m_3$, and $c \neq m_3$. If $a = m_3$, then there is a tree path from v_3 to u'_2 to a in $\mathcal{N}$, contradicting the choice of f . Thus $a \neq m_3$. In summary,

$$a \neq m_1 \neq m_2 \neq m_3, b \neq m_3, \text{ and } c \neq m_3.$$

We now consider two subcases:

- (i) Assume that $b \neq c$. By making the appropriate choices of reticulation arcs incident with v_1, v_2 , and v_3 , it is easily seen that $\mathcal{N}$ displays phylogenetic trees $\mathcal{T}_1, \mathcal{T}_2, \mathcal{T}_3$, and $\mathcal{T}_4$ such that

$$\begin{aligned} \mathcal{T}_1| \{a, m_1, m_2\} &\cong (a, m_1, m_2) \text{ and } \mathcal{T}_1| \{b, c, m_3\} \cong (m_3, b, c), \\ \mathcal{T}_2| \{a, m_1, m_2\} &\cong (a, m_1, m_2) \text{ and } \mathcal{T}_2| \{b, c, m_3\} \cong (m_3, c, b), \\ \mathcal{T}_3| \{a, m_1, m_2\} &\cong (a, m_2, m_1) \text{ and } \mathcal{T}_3| \{b, c, m_3\} \cong (m_3, b, c), \\ \mathcal{T}_4| \{a, m_1, m_2\} &\cong (a, m_2, m_1) \text{ and } \mathcal{T}_4| \{b, c, m_3\} \cong (m_3, c, b). \end{aligned}$$

Since $b \neq c$, we have that $\mathcal{T}_1, \mathcal{T}_2, \mathcal{T}_3$, and $\mathcal{T}_4$ are distinct, and so $|T(\mathcal{N})| \geq 4$, a contradiction.

- (ii) On the other hand, if $b = c$, then one of g_1 and g_2 , without loss of generality say g_2 , is a shortcut. As $\mathcal{N}$ has no 3-cycles, the vertex u'_3 has a child w that is neither u_3 nor v_3 . Let ℓ be a leaf at the end of a tree path that avoids u_3 and either starts at w if w is not a parent of a reticulation or starts at such a reticulation. Observe that $\ell \notin \{b, m_3\}$. By making the appropriate choices of reticulation arcs incident with v_1, v_2 , and v_3 , it is again easily seen that $\mathcal{N}$ displays phylogenetic trees $\mathcal{T}'_1, \mathcal{T}'_2, \mathcal{T}'_3$ and $\mathcal{T}'_4$ such that

$$\begin{aligned} \mathcal{T}'_1| \{a, m_1, m_2\} &\cong (a, m_1, m_2) \text{ and } \mathcal{T}'_1| \{b, \ell, m_3\} \cong (m_3, b, \ell), \\ \mathcal{T}'_2| \{a, m_1, m_2\} &\cong (a, m_1, m_2) \text{ and } \mathcal{T}'_2| \{b, \ell, m_3\} \cong (m_3, \ell, b), \\ \mathcal{T}'_3| \{a, m_1, m_2\} &\cong (a, m_2, m_1) \text{ and } \mathcal{T}'_3| \{b, \ell, m_3\} \cong (m_3, b, \ell), \\ \mathcal{T}'_4| \{a, m_1, m_2\} &\cong (a, m_2, m_1) \text{ and } \mathcal{T}'_4| \{b, \ell, m_3\} \cong (m_3, \ell, b). \end{aligned}$$

Since b, ℓ , and m_3 are distinct, it follows that $|T(\mathcal{N})| \geq 4$, another contradiction.

Hence if $|T(\mathcal{N} \setminus f)| = |T(\mathcal{N})| = 3$, then $\mathcal{N}$ is an octopus.

- (b) If $|T(\mathcal{N} \setminus f)| = 2$, then, by the previous base case, $\mathcal{N} \setminus f$ is an octopus. In particular, $\mathcal{N} \setminus f$ contains a 2-tight caterpillar ladder, say $\mathcal{N}'$.

Assume that $\mathcal{N}'$ is not a 2-tight caterpillar ladder of $\mathcal{N}$. Then $f = (u, v)$ is incident with one of the core arcs of $\mathcal{N}'$ in $\mathcal{N}$. If the head v of f is incident with such an arc, then $\mathcal{N}$ is not tree-child, a contradiction. If instead the tail u of f is incident with one of the core arcs of $\mathcal{N}'$ in $\mathcal{N}$, then this contradicts the choice of f . So $\mathcal{N}'$ is a 2-tight caterpillar ladder of $\mathcal{N}$ and f is not a core arc of this ladder.

Let v_1 and v_2 denote the reticulations of the 2-tight caterpillar ladder $\mathcal{N}'$ of $\mathcal{N}$, and assume that its core arcs are given by

$$\{(u'_2, u'_1), (u'_1, u_2), (u_2, u_1), (u'_1, v_1), (u_1, v_1), (u'_2, v_2), (u_2, v_2)\}.$$

Furthermore, let v_3 be the third reticulation of $\mathcal{N}$ and let $g_1 = (u_3, v_3)$ and $g_2 = (u'_3, v_3)$ denote the reticulation arcs of $\mathcal{N}$ directed into v_3 . For each $i \in \{1, 2, 3\}$, let m_i denote a leaf at the end of a tree path starting at v_i , and let a , b , and c denote a leaf at the end of a tree path starting at u_1 , u_3 , and u'_3 , respectively.

If $a \neq m_3$, we can apply the same arguments as in Cases (a)(i) and (a)(ii) to conclude that $|T(\mathcal{N})| \geq 4$, a contradiction. So we may assume that $a = m_3$, in which case, by the choice of f , there is a tree path from v_3 to u'_2 to a in $\mathcal{N}$. We now make a few observations. First, $m_1 \neq m_2 \neq a$. Second, if $b = m_1$, the path from v_1 to m_1 contains a reticulation, contradicting the fact that it is a tree path. Therefore $b \neq m_1$ and, similarly, $b \neq m_2$, $b \neq m_3$, $c \neq m_1$, $c \neq m_2$, and $c \neq m_3$. In summary,

$$m_1 \neq m_2 \neq m_3, b \notin \{m_1, m_2, m_3\}, c \notin \{m_1, m_2, m_3\}, \text{ and } a = m_3.$$

As in Case (a), we consider two subcases:

- (i) If $b \neq c$, then, as $b, c \notin \{a, m_1, m_2\}$, it follows as in Case (a)(i) that $|T(\mathcal{N})| \geq 4$, a contradiction.
- (ii) On the other hand, if $b = c$, then, one of g_1 and g_2 , without loss of generality say g_2 , is a shortcut. Since $\mathcal{N}$ has no 3-cycles, the vertex u'_3 has a child w that is neither u_3 nor v_3 . Let ℓ be a leaf at the end of a tree path avoiding u'_2 and either starting at w if w is not the parent of a reticulation or starting at such a reticulation. Observe that such a leaf exists and $\ell \notin \{b, m_3\}$. By the placement of v_3 , we have $\ell \notin \{a, m_1, m_2\}$. It is now easily checked that $\mathcal{N}$ displays phylogenetic trees $\mathcal{T}_1''$, $\mathcal{T}_2''$, $\mathcal{T}_3''$ and $\mathcal{T}_4''$ such that

$$\begin{aligned} \mathcal{T}_1''|_{\{a, m_1, m_2\}} &\cong (a, m_1, m_2) \text{ and } \mathcal{T}_1''|_{\{a, b, \ell\}} \cong (a, b, \ell), \\ \mathcal{T}_2''|_{\{a, m_1, m_2\}} &\cong (a, m_1, m_2) \text{ and } \mathcal{T}_2''|_{\{a, b, \ell\}} \cong (b, \ell, a), \\ \mathcal{T}_3''|_{\{a, m_1, m_2\}} &\cong (a, m_2, m_1) \text{ and } \mathcal{T}_3''|_{\{a, b, \ell\}} \cong (a, b, \ell), \\ \mathcal{T}_4''|_{\{a, m_1, m_2\}} &\cong (a, m_2, m_1) \text{ and } \mathcal{T}_4''|_{\{a, b, \ell\}} \cong (b, \ell, a). \end{aligned}$$

Since a , b , and ℓ are distinct, it follows that $|T(\mathcal{N})| \geq 4$, a contradiction.

Hence $|T(\mathcal{N} \setminus f)| \neq 2$.

This completes the proof of the lemma. $\square$

Proof of Theorem 1.1. Without loss of generality, we may assume that, amongst all tree-child networks with n leaves, k reticulations, and no 3-cycles, $|T(\mathcal{N})|$ is minimised, in which case, by Lemma 3.2, $|T(\mathcal{N})| \leq t(n, k)$. By Lemma 4.1, the theorem holds for $k \in \{0, 1, 2, 3\}$. Now suppose that $k \geq 4$, and so $n \geq 5$, and the theorem holds for all tree-child networks with n leaves, at most $k - 1$ reticulations, and no 3-cycles.

Let p_B be a tree vertex of $\mathcal{N}$ that is a parent of a reticulation, say p_A , so that, amongst all such tree vertices, p_B has maximum distance to the root. Let A and B denote the leaf sets of the pendant subtrees of $\mathcal{N}$ obtained by deleting the outgoing arc of p_A and the outgoing arc of p_B that is not (p_B, p_A) , respectively. By maximality, A and B are well defined. Let $a \in A$ and $b \in B$, and let e_1 and e_2 denote the reticulation arcs of $\mathcal{N}$ directed into p_A , where $e_1 = (p_B, p_A)$. Note that e_1 is not a shortcut. Let q_A denote the parent of p_A that is not p_B , that is $e_2 = (q_A, p_A)$. By Lemma 3.5 and the minimality and induction assumptions, p_A is not normal and so e_2 is a shortcut. With this setup, the remainder of the proof is to show that e_1 is the first rung of a 2-tight or 3-tight caterpillar ladder of $\mathcal{N}$, and then use induction to show that $\mathcal{N}$ is an octopus.

Let $P_u = q_A, u_1, u_2, \dots, u_r, p_B$ be a directed path from q_A to p_B in $\mathcal{N}$. Since $\mathcal{N}$ has no 3-cycles, we have $r \geq 1$. We next show that, for all $i \in \{1, 2, \dots, r\}$, the vertex u_i is a tree vertex and the parent of a reticulation. Note that this will imply that P_u is the unique directed path from q_A to p_B . In fact, we eventually show that $r = 1$.

Consider u_1 . Since $\mathcal{N}$ is tree-child, u_1 is not a reticulation. Assume that there is a tree path from u_1 to a leaf ℓ avoiding p_B . Let $\mathcal{T} \in T(\mathcal{N})$. Then $\mathcal{T}$ uses e_1 if and only if $\mathcal{T}|_{\{a, b, \ell\}} \cong (a, b, \ell)$, and $\mathcal{T}$ uses e_2 if and only if either $\mathcal{T}|_{\{a, b, \ell\}} \cong (a, \ell, b)$ or $\mathcal{T}|_{\{a, b, \ell\}} \cong (b, \ell, a)$. In particular, if $\mathcal{T}_1, \mathcal{T}_2 \in T(\mathcal{N})$, and $\mathcal{T}_1$ uses e_1 and $\mathcal{T}_2$ uses e_2 , then $\mathcal{T}_1$ and $\mathcal{T}_2$ are not isomorphic (an argument that we use repeatedly throughout the proof). Thus

$$|T(\mathcal{N})| = |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus e_1)|.$$

If $\mathcal{N} \setminus e_2$ has a 3-cycle and f is a reticulation arc of this 3-cycle, then, by Lemma 3.3, $\mathcal{N} \setminus \{e_2, f\}$ has no 3-cycles. Therefore, as $\mathcal{N} \setminus e_1$ has no 3-cycle, it follows by induction and Lemma 3.1(v) that

$$|T(\mathcal{N})| \geq t(n, k - 1) + t(n, k - 2) > t(n, k),$$

a contradiction to the minimality of $|T(\mathcal{N})|$. Thus there is no such tree path from u_1 . Instead, as $\mathcal{N}$ is tree-child, all tree paths from u_1 to a leaf traverse p_B . This implies that P_u has no reticulations and, for all $i \in \{1, 2, \dots, r\}$, the vertex u_i is a parent of a reticulation, v_i say. For each $i \in \{1, 2, \dots, r\}$, let m_i denote a leaf at the end of a tree path starting at v_i and observe that $m_i \notin A \cup B$. Furthermore, let u'_i denote the second parent of v_i , and let $f_i = (u_i, v_i)$ and $f'_i = (u'_i, v_i)$. By Lemma 3.5 and the minimality and induction assumptions, v_i is not normal for all i , and so either f_i or f'_i is a shortcut.

4.1.1. For all $i \in \{1, 2, \dots, r\}$, the arc f'_i is a shortcut and there is a directed path from u'_i to q_A .

Assume that, for some i , both u_i and u'_i lie on P_u . Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses e_1 , then $\mathcal{T}|\{a, b, m_i\} \cong (a, b, m_i)$. But, if $\mathcal{T}$ uses e_2 , then $\mathcal{T}|\{a, b, m_i\} \cong (b, m_i, a)$. Therefore

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus e_1)|.$$

Noting that $\mathcal{N} \setminus e_2$ may contain a 3-cycle, in which case, by Lemma 3.3, deleting one further arc results in a tree-child network with no 3-cycles, it follows by induction and Lemma 3.1(v) that

$$|T(\mathcal{N})| \geq t(n, k-2) + t(n, k-1) > t(n, k).$$

Hence, for all $i \in \{1, 2, \dots, r\}$, the vertex u'_i does not lie on P_u and so, as v_i is not normal, (u'_i, v_i) is a shortcut and there is a directed path from u'_i to q_A for all i . This proves (4.1.1).

4.1.2. $r = 1$.

Assume that $r \geq 2$. Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses e_1 , then $A \cup B$ is a cluster of $\mathcal{T}$. Also, if $\mathcal{T}$ uses $\{e_2, f_1, f'_2\}$ or $\{e_2, f'_1, f_2\}$, then $\mathcal{T}|\{a, b, m_1, m_2\} \cong (b, m_1, a, m_2)$ and $\mathcal{T}|\{a, b, m_1, m_2\} \cong (b, m_2, a, m_1)$, respectively. Observing that if $\mathcal{T}|\{a, b, m_1, m_2\}$ is isomorphic to either (b, m_1, a, m_2) or (b, m_2, a, m_1) , then $A \cup B$ is not a cluster of $\mathcal{T}$, it follows that

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus \{e_1, f'_1, f_2\})| + |T(\mathcal{N} \setminus \{e_1, f_1, f'_2\})|.$$

Say $\mathcal{N} \setminus e_2$ has no 3-cycle. If $k \geq 6$, then, as $\mathcal{N} \setminus \{e_1, f_1\}$ and $\mathcal{N} \setminus \{e_1, f_2\}$ have no 3-cycles, it follows by induction and Lemmas 3.1(v) and 3.3 that

$$\begin{aligned} |T(\mathcal{N})| &\geq t(n, k-1) + t(n, k-4) + t(n, k-4) \\ &= t(n, k-1) + t(n, k-2) \\ &> t(n, k). \end{aligned}$$

Furthermore, if $k = 4$, then

$$|T(\mathcal{N})| \geq t(n, 3) + t(n, 0) + t(n, 0) = 3 + 1 + 1 > 4 = t(n, 4)$$

while, if $k = 5$, then

$$|T(\mathcal{N})| \geq t(n, 4) + t(n, 1) + t(n, 1) = 4 + 2 + 2 > 6 = t(n, 5).$$

On the other hand, if $\mathcal{N} \setminus e_2$ has a 3-cycle, then, by construction, this 3-cycle contains the reticulation arcs f_1 and f'_1 , and so $\mathcal{N} \setminus f'_1$ has no 3-cycles. Thus, if $k \geq 6$, then, by induction and Lemmas 3.1(v) and 3.3,

$$\begin{aligned} |T(\mathcal{N})| &\geq t(n, k-2) + t(n, k-3) + t(n, k-4) \\ &> t(n, k-2) + t(n, k-2) \\ &= t(n, k). \end{aligned}$$

Also, if $k = 4$, then

$$|T(\mathcal{N})| \geq t(n, 2) + t(n, 1) + t(n, 0) = 2 + 2 + 1 > 4 = t(n, 4)$$

while, if $k = 5$, then

$$|T(\mathcal{N})| \geq t(n, 3) + t(n, 2) + t(n, 1) = 3 + 2 + 2 > 6 = t(n, 5).$$

These contradictions to the minimality of $|T(\mathcal{N})|$ imply that $r = 1$, thereby proving (4.1.2).

To simplify notation, set $u = u_1$, $u' = u'_1$, $v = v_1$, $m_u = m_1$, $f_u = f_1$, and $f'_u = f'_1$.

4.1.3. *If (u', q_A) is an arc of $\mathcal{N}$, then $\mathcal{N}$ is an octopus.*

Assume that (u', q_A) is an arc of $\mathcal{N}$. Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses $\{e_1, f_u\}$, then $\mathcal{T}|\{a, b, m_u\} \cong (a, b, m_u)$, while if $\mathcal{T}$ uses $\{e_2, f_u\}$, then $\mathcal{T}|\{a, b, m_u\} \cong (b, m_u, a)$. So

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus \{e_2, f'_u\})| + |T(\mathcal{N} \setminus \{e_1, f'_u\})|.$$

By induction and Lemma 3.1(v) and 3.3,

$$|T(\mathcal{N})| \geq t(n, k-2) + t(n, k-2) = t(n, k).$$

Therefore, as $|T(\mathcal{N})| \leq t(n, k)$,

$$|T(\mathcal{N})| = 2 \cdot t(n, k-2) = t(n, k). \quad (1)$$

We now show that $\mathcal{N}$ is an octopus. Since $\{u', q_A, u, p_B, p_A, v\}$ induces the core of a 2-tight caterpillar ladder of $\mathcal{N}$, it follows by Lemma 2.2 that f'_u is non-essential. Thus

$$|T(\mathcal{N})| = |T(\mathcal{N} \setminus f'_u)|.$$

In turn, it is now easily checked that

$$|T(\mathcal{N})| = 2|T(\mathcal{N} \setminus \{f'_u, e_2\})|$$

and so, by (1),

$$|T(\mathcal{N} \setminus \{f'_u, e_2\})| = t(n, k-2).$$

Therefore, by induction, $\mathcal{N} \setminus \{f'_u, e_2\}$ is an octopus, and so, by construction, $\mathcal{N}$ is an octopus. This proves (4.1.3).

Now assume that (u', q_A) is not an arc of $\mathcal{N}$. Let $P_t = u', t_1, t_2, \dots, t_s, q_A$ be a directed path from u' to q_A in $\mathcal{N}$. Similar to before, we will show that $s = 1$ and t_1 is the parent of a reticulation. Consider t_1 . Since $\mathcal{N}$ is tree-child, t_1 is not a reticulation. Say that there is a tree path from t_1 to a leaf ℓ avoiding q_A . Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses $\{e_1, f_u\}$, then $\mathcal{T}|\{a, b, m_u, \ell\} \cong (a, b, m_u, \ell)$. If $\mathcal{T}$ uses either $\{e_2, f_u\}$ or $\{e_2, f'_u\}$, then $\mathcal{T}|\{a, b, m_u, \ell\} \cong (b, m_u, a, \ell)$ and $\mathcal{T}|\{a, b, m_u, \ell\} \in \{(a, b, \ell, m_u), \{(a, b), (m_u, \ell)\}\}$, respectively. So

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus \{e_2, f'_u\})| + |T(\mathcal{N} \setminus \{e_1, f'_u\})| + |T(\mathcal{N} \setminus \{e_1, f_u\})|.$$

Now $\mathcal{N} \setminus e_2$ has no 3-cycle as u' is not the parent of q_A . Therefore, if $k \geq 5$, it follows by induction and Lemmas 3.1(v) and 3.3 that

$$\begin{aligned} |T(\mathcal{N})| &\geq t(n, k-3) + t(n, k-3) + t(n, k-2) \\ &= t(n, k-1) + t(n, k-2) \\ &> t(n, k), \end{aligned}$$

a contradiction. Furthermore, if $k = 4$, then

$$|T(\mathcal{N})| \geq t(n, 1) + t(n, 1) + t(n, 2) = 2 + 2 + 2 > 4 = t(n, k),$$

another contradiction. Thus there is no such tree path from t_1 , and so all tree paths from t_1 to a leaf traverse q_A . In turn, this implies that P_t has no reticulations, and so P_t consists of tree vertices and, for all $i \in \{1, 2, \dots, s\}$, the vertex t_i is a parent of a reticulation, w_i say. For each $i \in \{1, 2, \dots, s\}$, let m_i denote the leaf at the end of a tree path starting at w_i . Also let t'_i denote the second parent of w_i , and let $g_i = (t_i, w_i)$ and $g'_i = (t'_i, w_i)$. By Lemma 3.5, and the minimality and induction assumptions, either g_i or g'_i is a shortcut for all i .

4.1.4. *For all $i \in \{1, 2, \dots, s\}$, the arc g'_i is a shortcut and there is a directed path from t'_i to u' .*

Assume that, for some i , both t_i and t'_i lie on P_t . Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses $\{e_2, f'_u\}$, then $\mathcal{T}[\{a, b, m_u, m_i\}] \cong (a, b, m_i, m_u)$. Furthermore, if $\mathcal{T}$ uses $\{e_1, f_u\}$, then $\mathcal{T}[\{a, b, m_u, m_i\}] \cong (a, b, m_u, m_i)$, while if $\mathcal{T}$ uses $\{e_2, f_u\}$, then $\mathcal{T}[\{a, b, m_u, m_i\}] \cong (b, m_u, a, m_i)$. Thus

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus \{e_1, f_u\})| + |T(\mathcal{N} \setminus \{e_2, f'_u\})| + |T(\mathcal{N} \setminus \{e_1, f'_u\})|.$$

Noting that $\mathcal{N} \setminus f'_u$ may contain a 3-cycle but $\mathcal{N} \setminus e_2$ does not contain a 3-cycle, it follows by induction and Lemmas 3.1(v) and 3.3 that, if $k \geq 5$, then

$$\begin{aligned} |T(\mathcal{N})| &\geq t(n, k-2) + t(n, k-3) + t(n, k-3) \\ &= t(n, k-2) + t(n, k-1) \\ &> t(n, k), \end{aligned}$$

a contradiction. Also, if $k = 4$, then

$$|T(\mathcal{N})| \geq t(n, 2) + t(n, 1) + t(n, 1) = 2 + 2 + 2 > 4 = t(n, 4),$$

another contradiction. Thus, for all $i \in \{1, 2, \dots, s\}$, the vertex t'_i does not lie on P_t , and so g'_i is a shortcut and there is a directed path from t'_i to u' for all i . This proves (4.1.4).

4.1.5. $s = 1$.

Assume that $s \geq 2$. Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses e_1 , then $A \cup B$ is a cluster of $\mathcal{T}$. Also, if $\mathcal{T}$ uses $\{e_2, f_u\}$, then $\mathcal{T}[\{a, b, m_u\}] \cong (b, m_u, a)$. Furthermore, if $\mathcal{T}$ uses $\{e_2, f_u, g_1, g'_2\}$ or $\{e_2, f_u, g'_1, g_2\}$, then $\mathcal{T}[\{a, b, m_u, m_1, m_2\}] \cong (b, m_u, a, m_1, m_2)$ and $\mathcal{T}[\{a, b, m_u, m_1, m_2\}] \cong (b, m_u, a, m_2, m_1)$, respectively. Therefore

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus \{e_1, f'_u\})| \tag{2}$$

and

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus \{e_1, f'_u, g'_1, g_2\})| + |T(\mathcal{N} \setminus \{e_1, f'_u, g_1, g'_2\})|. \tag{3}$$

If $\mathcal{N} \setminus f'_u$ has a 3-cycle, then, by construction, this 3-cycle contains g_1 and g'_1 , in which case, by Lemma 3.3, neither $\mathcal{N} \setminus \{f'_u, g_1\}$ nor $\mathcal{N} \setminus \{f'_u, g'_1\}$ has a 3-cycle. Moreover, none of $\mathcal{N} \setminus e_2$, $\mathcal{N} \setminus g_1$, and $\mathcal{N} \setminus g_2$ has a 3-cycle. Therefore, if k is even, then, by (2), induction, and Lemmas 3.1(vi) and 3.3,

$$\begin{aligned} |T(\mathcal{N})| &\geq t(n, k-1) + t(n, k-3) \\ &> t(n, k), \end{aligned}$$

a contradiction. If $k \geq 7$ and odd, then, by (3), induction, Lemma 3.1(v) and (vi), and Lemma 3.3,

$$\begin{aligned} |T(\mathcal{N})| &\geq t(n, k-1) + t(n, k-4) + t(n, k-5) \\ &> t(n, k-1) + t(n, k-3) \\ &= t(n, k), \end{aligned}$$

while if $k = 5$, then

$$|T(\mathcal{N})| \geq t(n, 4) + t(n, 1) + t(n, 0) = 4 + 2 + 2 > 6 = t(n, 5).$$

These contradictions imply that $s = 1$, thereby proving (4.1.5).

To simplify (for the last time) the notation, set $t = t_1$, $t' = t'_1$, $w = w_1$, $m_t = m_1$, $g_t = g_1$, and $g'_t = g'_1$.

4.1.6. *If (t', u') is an arc of $\mathcal{N}$, then $\mathcal{N}$ is an octopus.*

Assume that (t', u') is an arc of $\mathcal{N}$. Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses e_1 , then $A \cup B$ is a cluster of $\mathcal{T}$, while if $\mathcal{T}$ uses $\{e_2, f_u\}$, then $\mathcal{T} \setminus \{a, b, m_u\} \cong (b, m_u, a)$. So

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus \{e_1, f'_u\})|.$$

Since $\mathcal{N} \setminus \{e_2, f'_u, g'_t\}$ has no 3-cycles by Lemma 3.3, it follows by induction that

$$|T(\mathcal{N})| \geq t(n, k-1) + t(n, k-3).$$

If k is even, then, by Lemma 3.1(vi), we have $|T(\mathcal{N})| > t(n, k)$, a contradiction. So say $k \geq 5$ and odd. Then, as $|T(\mathcal{N})| \leq t(n, k)$,

$$|T(\mathcal{N})| = t(n, k-1) + t(n, k-3) = t(n, k).$$

We now show that $\mathcal{N}$ is an octopus. Since $\{t', u', t, q_A, u, p_B, w, v, p_A\}$ induces the core of a 3-tight caterpillar ladder of $\mathcal{N}$, it follows by Lemma 2.2 that g'_t is non-essential. Thus

$$|T(\mathcal{N})| = |T(\mathcal{N} \setminus g'_t)|.$$

In turn, it is easily checked that

$$|T(\mathcal{N})| = 3 \cdot |T(\mathcal{N} \setminus \{g'_t, f'_u, e_2\})|.$$

Therefore, by induction,

$$t(n, k-1) + t(n, k-3) = |T(\mathcal{N})| = 3 \cdot |T(\mathcal{N} \setminus \{g'_t, f'_u, e_2\})| \geq 3 \cdot t(n, k-3),$$

that is, as $k \geq 5$, and thus, by Lemma 3.1(v), $t(n, k - 1) = 2 \cdot t(n, k - 3)$, we have

$$|T(\mathcal{N} \setminus \{g'_t, f'_u, e_2\})| = t(n, k - 3).$$

Hence, by induction, $\mathcal{N} \setminus \{g'_t, f'_u, e_2\}$ is an octopus with an even number of reticulations. It follows by construction that $\mathcal{N}$ is an octopus, completing the proof of (4.1.6).

Thus we may now assume that (t', u') is not an arc. Let $\mathcal{T} \in T(\mathcal{N})$. If $\mathcal{T}$ uses e_1 , then $A \cup B$ is cluster of $\mathcal{T}$, while if $\mathcal{T}$ uses $\{e_2, f_u\}$, then $A \cup B$ is not a cluster of $\mathcal{T}$. Thus

$$|T(\mathcal{N})| \geq |T(\mathcal{N} \setminus e_2)| + |T(\mathcal{N} \setminus \{e_1, f'_u\})|.$$

Since (t', u') is not an arc, $\mathcal{N} \setminus \{e_1, f'_u\}$ has no 3-cycles and so, by induction and Lemma 3.1(v),

$$|T(\mathcal{N})| \geq t(n, k - 1) + t(n, k - 2) > t(n, k).$$

This last contradiction completes the proof of the theorem. □

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