



Asymptotic enumeration of rooted binary unlabeled galled trees with a fixed number of galls

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Abstract

Galled trees appear in problems concerning admixture, horizontal gene transfer, hybridization, and recombination. Building on a recursive enumerative construction, we study the asymptotic behavior of the number of rooted binary unlabeled (normal) galled trees as the number of leaves n increases, maintaining a fixed number of galls g . We find that the exponential growth with n of the number of rooted binary unlabeled normal galled trees with g galls has the same value irrespective of the value of $g \geq 0$. The subexponential growth, however, depends on g ; it follows $c_g n^{2g-3/2}$, where c_g is a constant dependent on g . Although for each g , the exponential growth is approximately 2.4833^n , summing across *all* g , the exponential growth is instead approximated by the much larger 4.8230^n .

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1 Introduction

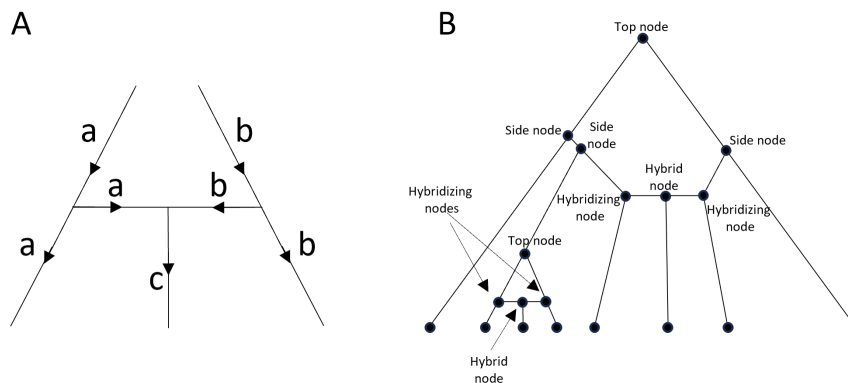
Rooted binary trees are a staple of mathematical phylogenetic analysis, as they are used to represent diverse biological processes taking place in time—including the evolution of species, the evolution of genes among those species, and the divergence of populations [9, 20, 23]. The root represents a common ancestor, and the leaves represent subsequent biological entities, often in the present day. Viewed as objects evolving in time, by extension of “vertical” inheritance that occurs in genetic transmission from parents to offspring, biological divergences are viewed as taking place vertically on the tree. Mathematical phylogenetic analyses of trees have produced rich contributions to algorithmic and combinatorial studies.

Certain evolutionary events, however, involve *merging* rather than *divergence* of biological lineages. Such events include the recombination that occurs during gamete formation, population admixture, horizontal gene transfer, and hybridization. To describe processes that include these events, we must look beyond trees to *phylogenetic networks* [13, 16, 17].

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■ **Figure 1** Features of a gall in a galled tree. (A) A gall as a representation of a biological merging event. Biological lineages a and b each bifurcate, with one branch of each bifurcation merging to form lineage c . (B) Nomenclature for the various nodes in a gall.

41 Among the phylogenetic networks, galled trees are some of the simplest. As their name
 42 suggests, they are tree-like, but they can contain certain internal nodes with in-degree 2
 43 and out-degree 1, representing permitted classes of mergings. Galled trees are named for
 44 the growths, termed *galls*, which appear in plants but which do not disrupt their tree-like
 45 structure. They were first introduced in the study of recombination [14, 15, 22].

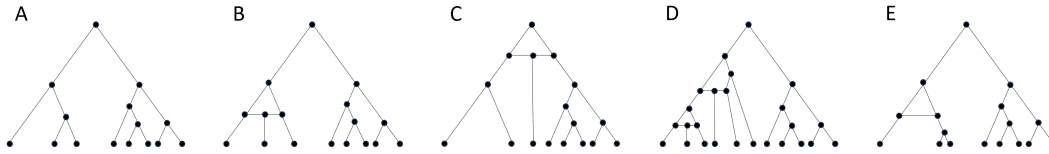
46 Mathematically, a galled tree allows each vertex or edge in a graph to be contained in at
 47 most one cycle. An additional requirement is needed for galled trees to be meaningful for
 48 biological processes such as hybridization. In a hybridization event, two biological lineages, a
 49 and b , each bifurcate; a merging event occurs between two branches, one from each bifurcation,
 50 producing a third lineage, c (Figure 1A). The structure of the event requires that when
 51 viewed graphically, a gall—a cycle in the graph—contains at least four nodes. These include
 52 a *top node*, two *hybridizing nodes*, and one *hybrid node*. Additional *side nodes* are permitted,
 53 and we regard the hybridizing nodes as special side nodes (Figure 1B). The requirement that
 54 galls have at least four nodes is equivalent to a requirement that galled trees be *normal*.

55 Many enumerative problems on galled trees have been investigated; [3, 4, 5, 12, 19, 21],
 56 this study concerns rooted binary unlabeled normal galled trees. Given number of galls g , as
 57 the number of leaves $n \rightarrow \infty$, what is the growth of the size of this class? The case of $g = 0$
 58 is the enumeration of rooted binary unlabeled trees, and we previously studied $g = 1$ [1].
 59 Building on a recurrence for rooted binary unlabeled normal galled trees with n leaves and
 60 g galls, we obtain a generating function for $g = 2$. We find the asymptotic behavior of the
 61 number of trees with n leaves and $g = 2$ galls, and we obtain asymptotics for each $g > 2$.

62 2 Definitions

63 We define our concepts formally. We assume that all networks and trees are binary; we
 64 usually drop the term *binary*. A *rooted phylogenetic network* is a directed acyclic graph in
 65 which four properties hold. (i) There exists a unique node with in-degree 0 and out-degree
 66 2. This node is the *root node*. (ii) *Leaf nodes* possess in-degree 1 and out-degree 0. (iii)
 67 Non-leaf, non-root nodes possess in-degree 2 and out-degree 1 or in-degree 1 and out-degree
 68 2. (iv) Edges are directed away from the root. Nodes with in-degree 2 and out-degree 1 are
 69 *reticulation nodes* (or *hybrid nodes*). Nodes with in-degree 1 and out-degree 2 are *tree nodes*.

70 A *rooted galled tree* is a rooted phylogenetic network with three additional properties. (v)
 71 Each reticulation node a_r has a unique ancestor node r so that exactly two non-overlapping



■ **Figure 2** Rooted binary unlabeled galled trees. (A) A tree with no galls. (B) A galled tree with one gall. (C) A galled tree with a root gall. (D) A galled tree with two galls. (E) A galled tree that is not a normal galled tree and that is not included in the class of galled trees that we enumerate.

72 paths of edges connect r to a_r . Ignoring the direction of the edges, the two paths from r to
 73 a_r produce a cycle C_r . The cycle is termed a *gall*. (vi) Consider galls C_r and C_s , associated
 74 with reticulation nodes a_r and a_s , $a_r \neq a_s$. The sets of nodes in the galls C_r and C_s
 75 are disjoint. (vii) Ancestor node r and reticulation node a_r are separated by two or more edges.
 76 Condition (vii) encodes the requirement that we consider only *normal* galled trees (Figure 2).

77 We generally drop the terms *rooted* and *normal*, and refer only to *galled trees*, and where
 78 a distinction is necessary, *labeled* and *unlabeled* galled trees. Although a galled tree is not
 79 technically a tree due to the presence of cycles, we continue to refer to galled trees as trees.
 80 We similarly refer to the galled trees rooted at internal nodes of a galled tree as *subtrees*. Our
 81 view of galls as representations of biological merging events leads us to depict hybridizing
 82 nodes and their associated hybrid node on a horizontal line, representing the simultaneity of
 83 these nodes when a galled tree is taken to represent a structure evolving in time [2, 19].

84 A basic result describes the maximal number of galls possible in a galled tree with n
 85 leaves. A gall contains three or more descendant subtrees: one from the reticulation node,
 86 two from the hybridizing nodes, and one for each additional side node. Hence, the smallest
 87 galled tree possesses $n = 3$ leaves. Adding a gall to a galled tree involves replacing one
 88 subtree with at least three subtrees, so that each gall adds at least two leaves. For a tree
 89 with g galls, the number of leaves satisfies $n \geq 2g + 1$, or $g \leq \lfloor \frac{n-1}{2} \rfloor$ [19].

90 We will need to consider *compositions*, ordered lists of positive integers that sum to a
 91 specified value. We denote by $C(a, b)$ the compositions of a natural number a into b parts.
 92 $C(a, b)$ is the set of ordered lists of positive integers of length b , (i_1, i_2, \dots, i_b) , with sum equal
 93 to a . We denote by $C_p(a, b)$ the subset of $C(a, b)$ containing the *palindromic* compositions of
 94 a , that is, the compositions (i_1, i_2, \dots, i_b) for which $i_j = i_{b-j+1}$ for each j from 1 to b .

95 3 Previous work

96 We review a number of results. The rooted binary unlabeled galled trees generalize the
 97 rooted binary unlabeled trees without galls. Letting U_n denote the number of rooted binary
 98 unlabeled trees with no galls and letting $\mathcal{U}(t)$ denote the generating function $\sum_{n \geq 0} U_n t^n$,

$$99 \quad \mathcal{U}(t) = t + \frac{1}{2}\mathcal{U}^2(t) + \frac{1}{2}\mathcal{U}(t^2). \quad (1)$$

100 Denoting the radius of convergence by ρ , as $t \rightarrow \rho^-$, we have $\mathcal{U}(t) \sim 1 - \gamma\sqrt{1 - t/\rho}$, where
 101 $\gamma \approx 1.1300$ and $\rho \approx 0.4027$ [8, p. 55] [10, pp. 476-477]. The asymptotic approximation for
 102 the number of rooted binary unlabeled trees (with no galls) is,

$$103 \quad U_n = [t^n]\mathcal{U}(t) \sim \frac{\gamma}{2\Gamma(\frac{1}{2})} n^{-\frac{3}{2}} \rho^{-n}. \quad (2)$$

104 In our previous work on rooted binary unlabeled normal galled trees [1] (henceforth
 105 “unlabeled galled trees”), we obtained a recursion enumerating the A_n unlabeled galled trees

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with n leaves and another recursion enumerating the $E_{n,g}$ unlabeled galled trees with a specified number of galls g . We specifically considered the case of $g = 1$. We also studied the asymptotics of A_n and $E_{n,1}$ through their generating functions. The generating function for unlabeled galled trees, considering all possible numbers of galls, was found to be [1, eq. 36]

$$\mathcal{A}(t) = t + \frac{1}{2}\mathcal{A}^2(t) + \frac{1}{2}\mathcal{A}(t^2) + 1 - \frac{1}{1-\mathcal{A}(t)} + \frac{\mathcal{A}(t)}{2[1-\mathcal{A}(t)]^2} + \frac{\mathcal{A}(t)}{2[1-\mathcal{A}(t^2)]}. \quad (3)$$

The three leftmost terms, identical to the generating function $\mathcal{U}(t)$ (eq. 1), arise from the galled trees in which two subtrees descend immediately from the root. The other terms arise from galled trees with a gall that contains the root, a *root gall*.

Using the *asymptotics of implicit tree-like classes* theorem [10, pp. 467-468], we obtained the asymptotics of the number of galled trees with n leaves, A_n [1, eq. 42]: $A_n = [t^n]\mathcal{A}(t) \sim [\delta/(2\Gamma(\frac{1}{2}))]n^{-\frac{3}{2}}\alpha^{-n}$, where $\delta \approx 0.2793$ and $\alpha \approx 0.2073$. $\mathcal{A}(t)$ has convergence radius about half that of $\mathcal{U}(t)$, so that galled trees are much more numerous than the trees without galls.

We also derived the generating function $\mathcal{E}_1(t)$ and asymptotic growth of the number of unlabeled galled trees with exactly one gall. We state these results as propositions.

► **Proposition 1.** [1, eq. 48] *The generating function $\mathcal{E}_1(t)$ for the number of unlabeled galled trees with 1 gall satisfies*

$$\mathcal{E}_1(t) = \frac{1}{1-\mathcal{U}(t)} - \frac{1}{[1-\mathcal{U}(t)]^2} + \frac{\mathcal{U}(t)}{2[1-\mathcal{U}(t)]^3} + \frac{\mathcal{U}(t)}{2[1-\mathcal{U}(t)][1-\mathcal{U}(t^2)]}. \quad (4)$$

► **Proposition 2.** [1, eq. 50] *The asymptotic growth of the number $E_{n,1}$ of unlabeled galled trees with n leaves and 1 gall satisfies*

$$E_{n,1} \sim \frac{1}{2\gamma^3\Gamma(\frac{3}{2})}n^{\frac{1}{2}}\rho^{-n} = \frac{1}{\gamma^3\sqrt{\pi}}n^{\frac{1}{2}}\rho^{-n}. \quad (5)$$

Proposition 2 follows from the fact that as $t \rightarrow \rho^-$, $\mathcal{E}_1(t) \sim 1/[2\gamma^3(1-t/\rho)^{\frac{3}{2}}]$. $\mathcal{E}_1(t)$ in eq. 4 depends on $\mathcal{U}(t)$. Eq. 5 clarifies that the exponential growth of the number of unlabeled galled trees with one gall is the same as that of the number of unlabeled galled trees with no galls; only the subexponential growth differs. We will generalize this result.

4 Galled trees with two galls, $E_{n,2}$

4.1 Recursion

In [1, eq. 27], we obtained a recursion for $E_{n,g}$, the number of unlabeled galled trees with n leaves and exactly g galls. The base cases are $E_{1,0} = 1$ and $E_{1,g} = 0$ for $g \geq 1$. We also write $E_{m,\ell} = 0$ when m is not a positive integer, ℓ is not a positive integer, or both.

► **Proposition 3.** *For (n, g) with $n \geq 2$ and $0 \leq g \leq \lfloor \frac{n-1}{2} \rfloor$, the number of unlabeled galled trees with n leaves and g galls is*

$$E_{n,g} = \frac{1}{2} \left[\left(\sum_{\mathbf{c} \in C(n,2)} \sum_{\mathbf{d} \in C(g+2,2)} \prod_{i=1}^2 E_{c_i, d_i-1} \right) + E_{\frac{n}{2}, \frac{g}{2}} \right] \quad (6)$$

$$+ \left(\sum_{k=3}^n (k-2) \sum_{\mathbf{c} \in C(n,k)} \sum_{\mathbf{d} \in C(g-1+k,k)} \prod_{i=1}^k E_{c_i, d_i-1} \right) \quad (7)$$

$$+ \left(\sum_{a=1}^{\lfloor \frac{n-1}{2} \rfloor} \sum_{\mathbf{c} \in C_p(n,2a+1)} \sum_{\mathbf{d} \in C_p(g-1+2a+1,2a+1)} \prod_{i=1}^{a+1} E_{c_i, d_i-1} \right). \quad (8)$$

140 The approach is to use a recursion at the root node. We sum over all products of possible
 141 counts of subtrees, each with fewer than n leaves. Pairs of galled trees that are reflections of
 142 one another over the root—or the axis connecting the top node to the reticulation node of
 143 the root gall—are the same unlabeled galled tree, explaining the leading $\frac{1}{2}$. We add back
 144 terms for galled trees that are symmetric over the root, which are not double-counted.

145 Line 6 in Proposition 3 enumerates galled trees with n leaves and g galls that do not have
 146 a root gall. The first term traverses combinations of numbers of leaves in the two subtrees
 147 summing to n by traversing compositions \mathbf{c} of n into 2 parts ($\mathbf{c} \in C(n, 2)$). It also traverses
 148 combinations of placements of the g galls in the two subtrees. Because subtrees can possess
 149 0 galls, these combinations are identified from compositions of $g + 2$ into 2 parts, subtracting
 150 1 gall in each part of the composition ($\mathbf{d} \in C(g + 2, 2)$). The second term adds back the
 151 galled trees with identical subtrees; this term is nonzero only if both n and g are even.

152 Line 7 counts galled trees with n leaves and g galls that do have a root gall. It traverses
 153 the possible number k of subtrees descending from side nodes, hybridizing nodes, and the
 154 hybrid node of the root gall (3 to n , the number of leaves). It then traverses the $k - 2$ possible
 155 nodes in the root gall where the hybrid node can be placed: all k nodes except immediate
 156 descendants of the root. We then traverse the possible combinations of the n leaves and $g - 1$
 157 remaining (non-root) galls into the k subtrees, again allowing subtrees with no galls.

158 Line 8 adds back half the galled trees with n leaves and g galls that have a root gall and
 159 that are symmetric over the reticulation node. Here, a is the possible number of subtrees of
 160 the root gall on each side of the reticulation node, so that the root gall has $2a + 1$ subtrees in
 161 total. The composition of the n leaves into $2a + 1$ subtrees and the composition of the $g - 1$
 162 galls into those subtrees are both palindromic. Given these compositions, a tree is specified
 163 by its subtrees of one side of the reticulation node and the subtree of the reticulation node.

164 For $g = 2$, for $n \geq 2$, the recursion for $E_{n,g}$ becomes

$$\begin{aligned}
 165 \quad E_{n,2} &= \frac{1}{2} \left[\left(\sum_{c=1}^{n-1} \sum_{d=0}^2 E_{c,d} E_{n-c,2-d} \right) + E_{\frac{n}{2},1} \right. \\
 166 \quad &+ \sum_{k=3}^n (k-2) \sum_{\mathbf{c} \in C(n,k)} \sum_{\mathbf{d} \in C(k+1,k)} \prod_{i=1}^k E_{c_i,d_i-1} \\
 167 \quad &+ \left. \sum_{a=1}^{\lfloor \frac{n-1}{2} \rfloor} \sum_{\mathbf{c} \in C_p(n,2a+1)} \sum_{\mathbf{d} \in C_p(2a+2,2a+1)} \prod_{i=1}^{a+1} E_{c_i,d_i-1} \right] \\
 168 \quad &= \frac{1}{2} \left[\left(2 \sum_{m=1}^{n-1} U_m E_{n-m,2} + \sum_{m=1}^{n-1} E_{m,1} E_{n-m,1} \right) + E_{\frac{n}{2},1} \right. \\
 169 \quad &+ \sum_{k=3}^n (k-2) \sum_{m=k-1}^{n-1} \sum_{\mathbf{c} \in C(m,k-1)} \left(\prod_{i=1}^{k-1} U_{c_i} \right) k E_{n-m,1} \\
 170 \quad &+ \left. \sum_{a=1}^{\lfloor \frac{n-1}{2} \rfloor} \sum_{\mathbf{c} \in C_p(n,2a+1)} \left(\prod_{i=1}^a U_{c_i} \right) E_{c_{a+1},1} \right]. \tag{9}
 \end{aligned}$$

171 Recall here that $E_{m,1} = 0$ if $m \notin \mathbb{N}$. In the first line, m gives the number of leaves in the
 172 “left” subtree of the root and $n - m$ is the number in the “right” subtree (the left–right
 173 distinction is solely for convenience). In the second line, k is the number of subtrees of the
 174 root gall, m is the number of leaves across the $k - 1$ subtrees of the root gall that *do not*
 175 contain a gall, and $n - m$ is the number of leaves in the subtree with the second gall.

198 ► **Proposition 4.** *The generating function $\mathcal{E}_2(t)$ for the number of unlabeled galled trees with*
 199 *2 galls satisfies*

$$200 \quad \mathcal{E}_2(t) = \frac{\mathcal{E}_1(t)}{2[1-\mathcal{U}(t)]} \left[\mathcal{E}_1(t) + \frac{\mathcal{U}(t) + \mathcal{U}^2(t)}{[1-\mathcal{U}(t)]^3} - \frac{1}{1-\mathcal{U}(t)} + \frac{1}{1-\mathcal{U}(t^2)} \right] + \frac{\mathcal{E}_1(t^2)}{2[1-\mathcal{U}(t)]}. \quad (14)$$

201 4.3 Asymptotic analysis

202 To analyze the asymptotics of $\mathcal{E}_2(t)$ as $t \rightarrow \rho^-$, we take the highest-order terms in Proposition
 203 4, that is, the terms with the highest power of $1 - t/\rho$ in the denominator. We recall
 204 $\mathcal{U}(t) \sim 1 - \gamma\sqrt{1 - t/\rho}$. From Proposition 1, $\mathcal{E}_1(t) \sim 1/[2\gamma^3(1 - t/\rho)^{\frac{3}{2}}]$. We have:

$$205 \quad \mathcal{E}_2(t) \sim \frac{\mathcal{E}_1^2(t)}{2[1-\mathcal{U}(t)]} + \frac{2\mathcal{E}_1(t)}{2[1-\mathcal{U}(t)]^4} = \frac{5}{8\gamma^7(1 - t/\rho)^{7/2}}. \quad (15)$$

206 To obtain a result for the coefficients $E_{n,2}$, we use the transfer formula (Corollary VI.1, page
 207 392 and Theorem VI.4, page 393 in [10])—according to which, if $f(t)$ is Δ -analytic with a
 208 singularity at b , and $f(t) \sim (1 - \frac{t}{b})^{-a}$ as $\frac{t}{b} \rightarrow 1$ with t in Δ , and $a \notin \{0, -1, -2, \dots\}$, then
 209 $[t^n]f(t) \sim n^{a-1}b^{-n}/\Gamma(a)$. Here, ρ fulfills the role of b and $\frac{7}{2}$ that of a .

210 ► **Proposition 5.** *The asymptotic growth of the number $E_{n,2}$ of unlabeled galled trees with n*
 211 *leaves and 2 galls satisfies*

$$212 \quad E_{n,2} \sim \frac{5}{8\gamma^7\Gamma(\frac{7}{2})}n^{\frac{5}{2}}\rho^{-n} = \frac{1}{3\gamma^7\sqrt{\pi}}n^{\frac{5}{2}}\rho^{-n}. \quad (16)$$

213 We note the appearance of ρ^{-n} and $n^{5/2}$ to obtain the following corollary.

214 ► **Corollary 6.** *The exponential growth of $\mathcal{E}_2(t)$ is the same as that of $\mathcal{U}(t)$ and $\mathcal{E}_1(t)$; however,*
 215 *its subexponential growth is greater.*

216 5 Galled trees with g galls, $E_{n,g}$

217 5.1 Recursion

218 For fixed g , Proposition 3 gives the recursion for $E_{n,g}$. We proceed from this general case.

219 5.2 Generating function

220 We denote the generating function of the number of galled trees with exactly g galls by
 221 $\mathcal{E}_g(t) = \sum_{n \geq 0} E_{n,g}t^n$. From Proposition 3, we can decompose the generating function by

$$222 \quad \mathcal{E}_g(t) = \frac{1}{2} \left[\underbrace{\sum_{n \geq 0} \left(\left(\sum_{\mathbf{c} \in C(n,2)} \sum_{\mathbf{d} \in C(g+2,2)} \prod_{i=1}^2 E_{c_i, d_i-1} \right) + E_{\frac{n}{2}, \frac{g}{2}} \right) t^n}_{\mathcal{E}_{g_i}(t)} \right. \\
 223 \quad \left. + \underbrace{\sum_{n \geq 0} \left(\sum_{k=3}^n (k-2) \sum_{\mathbf{c} \in C(n,k)} \sum_{\mathbf{d} \in C(g-1+k,k)} \prod_{i=1}^k E_{c_i, d_i-1} \right) t^n}_{\mathcal{E}_{2ii}(t)} \right. \\
 224 \quad \left. + \underbrace{\sum_{n \geq 0} \left(\sum_{a=1}^{\lfloor \frac{n-1}{2} \rfloor} \sum_{\mathbf{c} \in C_p(n,2a+1)} \sum_{\mathbf{d} \in C_p(g-1+2a+1,2a+1)} \prod_{i=1}^{a+1} E_{c_i, d_i-1} \right) t^n}_{\mathcal{E}_{2iii}(t)} \right]. \quad (17)$$

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225 where $E_{n,g} = 0$ for pairs with $n = 0$ or $n = 1$ and $g \geq 1$. The terms in the decomposition are

$$\begin{aligned}
 226 \quad \mathcal{E}_{g_i}(t) &= 2 \sum_{m \geq 0} \sum_{n \geq m} (U_m t^m) (E_{n-m,g} t^{n-m}) + \sum_{j=1}^{g-1} \sum_{m \geq 0} \sum_{n \geq m} (E_{m,j} t^m) (E_{n-m,g-j} t^{n-m}) \\
 227 \quad &+ \sum_{n \geq 0} E_{\frac{n}{2}, \frac{g}{2}} t^n \\
 228 \quad \mathcal{E}_{g_{ii}}(t) &= \sum_{\ell=1}^{g-1} \sum_{k \geq 3} (k-2) \binom{k}{\ell} \sum_{m \geq k-\ell} \sum_{\mathbf{c} \in C(m, k-\ell)} \prod_{i=1}^{k-\ell} U_{c_i} t^{c_i} \\
 229 \quad &\times \sum_{n \geq m} \sum_{\tilde{\mathbf{c}} \in C(n-m, \ell)} \sum_{\mathbf{d} \in C(g-1, \ell)} \prod_{j=1}^{\ell} E_{\tilde{c}_j, d_j} t^{\tilde{c}_j} \tag{18} \\
 230 \quad \mathcal{E}_{g_{iii}}(t) &= \sum_{\ell=0}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{a \geq 1} \binom{a}{\ell} \sum_{m_1 \geq a-\ell} \sum_{\mathbf{c} \in C(m_1, a-\ell)} \prod_{i=1}^{a-\ell} U_{c_i} t^{2c_i} \\
 231 \quad &\times \sum_{m \geq m_1 + \ell} \sum_{\tilde{\mathbf{c}} \in C(m-m_1, \ell)} \sum_{b=\ell}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{\mathbf{d} \in C(b, \ell)} \prod_{j=1}^{\ell} E_{\tilde{c}_j, d_j} t^{2c_j} \sum_{n \geq 2m} E_{n-2m, g-1-2b} t^{n-2m}, \tag{19}
 \end{aligned}$$

232 where it is convenient to denote U_n by $E_{n,0}$ for terms with $g-1-2b=0$ in $\mathcal{E}_{g_{iii}}(t)$.

233 In $\mathcal{E}_{g_i}(t)$, j is the number of galls in the left subtree of the root, supposing both subtrees
 234 possess at least one gall. In $\mathcal{E}_{g_{ii}}(t)$, ℓ is the number of subtrees of the root gall that possess at
 235 least one gall; k is the number of subtrees of the root gall, so that $\binom{k}{\ell}$ counts ways to select
 236 which ℓ subtrees possess galls; and m is the number of leaves in the $k-\ell$ remaining subtrees.

237 Similarly, in $\mathcal{E}_{g_{iii}}(t)$, for symmetric root galls, ℓ is the number of subtrees of the left side
 238 of the root gall that contain galls; a is the number of subtrees of the left side of the root gall;
 239 m_1 is the sample size in the $a-\ell$ subtrees that do not possess galls; $m-m_1$ is the sample
 240 size in the ℓ subtrees that do possess galls; and b is the number of galls in those ℓ subtrees.

241 We now solve each part of the decomposition:

$$\begin{aligned}
 242 \quad \mathcal{E}_{g_i}(t) &= 2 \sum_{m \geq 0} (U_m t^m) \sum_{\ell \geq 0} (E_{\ell,g} t^\ell) + \sum_{j=1}^{g-1} \sum_{m \geq 0} (E_{m,j} t^m) \sum_{\ell \geq 0} (E_{\ell,g-j} t^\ell) + \sum_{n \geq 0} E_{n, \frac{g}{2}} t^{2n} \\
 243 \quad &= 2\mathcal{U}(t) \mathcal{E}_g(t) + \left(\sum_{j=1}^{g-1} \mathcal{E}_j(t) \mathcal{E}_{g-j}(t) \right) + \mathcal{E}_{\frac{g}{2}}(t^2). \tag{20}
 \end{aligned}$$

244 where $\mathcal{E}_\ell(t) = 0$ for $\ell \notin \mathbb{N}$. The second part produces

$$\begin{aligned}
 245 \quad \mathcal{E}_{g_{ii}}(t) &= \sum_{\ell=1}^{g-1} \sum_{k \geq \max(\ell, 3)} (k-2) \binom{k}{\ell} \sum_{i_1 \geq 0} \sum_{i_2 \geq 0} \dots \sum_{i_{k-\ell} \geq 0} U_{i_1} U_{i_2} \dots U_{i_{k-\ell}} t^{i_1+i_2+\dots+i_{k-\ell}} \\
 246 \quad &\times \sum_{\mathbf{d} \in C(g-1, \ell)} \sum_{j_1 \geq 0} \sum_{j_2 \geq 0} \dots \sum_{j_\ell \geq 0} E_{j_1, d_1} E_{j_2, d_2} \dots E_{j_\ell, d_\ell} t^{j_1+j_2+\dots+j_\ell} \\
 247 \quad &= \sum_{\ell=1}^{g-1} \left(\sum_{k \geq \max(\ell, 3)} (k-2) \binom{k}{\ell} \mathcal{U}^{k-\ell}(t) \right) \sum_{\mathbf{d} \in C(g-1, \ell)} \prod_{j=1}^{\ell} \mathcal{E}_{d_j}(t) \\
 248 \quad &= \sum_{\ell=1}^{g-1} \left(\frac{3\mathcal{U}(t) - 2 + \ell}{[1 - \mathcal{U}(t)]^{\ell+2}} + \llbracket \ell = 1 \rrbracket \right) \sum_{\mathbf{d} \in C(g-1, \ell)} \prod_{j=1}^{\ell} \mathcal{E}_{d_j}(t). \tag{21}
 \end{aligned}$$

249 Here, $\llbracket \cdot \rrbracket$ denotes the Iverson bracket. Finally, for the third part,

$$\begin{aligned}
 250 \quad \mathcal{E}_{g_{\text{iii}}}(t) &= \sum_{\ell=0}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{a \geq 1} \binom{a}{\ell} \sum_{i_1 \geq 0} \sum_{i_2 \geq 0} \cdots \sum_{i_{a-\ell} \geq 0} U_{i_1} U_{i_2} \cdots U_{i_{a-\ell}} t^{2i_1+2i_2+\dots+2i_{a-\ell}} \\
 251 \quad &\times \sum_{b=\ell}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{\mathbf{d} \in C(b,\ell)} \sum_{j_1 \geq 0} \sum_{j_2 \geq 0} \cdots \sum_{j_\ell \geq 0} E_{j_1, d_1} E_{j_2, d_2} \cdots E_{j_\ell, d_\ell} t^{2j_1+2j_2+\dots+2j_\ell} \\
 252 \quad &\times \sum_{j \geq 0} E_{j, g-1-2b} t^j \\
 253 \quad &= \sum_{\ell=0}^{\lfloor \frac{g-1}{2} \rfloor} \left(\sum_{a \geq 1} \binom{a}{\ell} \mathcal{U}^{a-\ell}(t^2) \right) \sum_{b=\ell}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{\mathbf{d} \in C(b,\ell)} \left(\prod_{j=1}^{\ell} \mathcal{E}_{d_j}(t^2) \right) \mathcal{E}_{g-1-2b}(t) \\
 254 \quad &= \sum_{\ell=0}^{\lfloor \frac{g-1}{2} \rfloor} \left(\frac{1}{[1-\mathcal{U}(t^2)]^{\ell+1}} - \llbracket \ell = 0 \rrbracket \right) \sum_{b=\ell}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{\mathbf{d} \in C(b,\ell)} \left(\prod_{j=1}^{\ell} \mathcal{E}_{d_j}(t^2) \right) \mathcal{E}_{g-1-2b}(t). \quad (22)
 \end{aligned}$$

255 **5.3 Asymptotic analysis**

256 $\mathcal{E}_g(t)$ is the sum $\frac{1}{2}[\mathcal{E}_{g_i}(t) + \mathcal{E}_{g_{\text{ii}}}(t) + \mathcal{E}_{g_{\text{iii}}}(t)]$ (eq. 17). We denote $\mathcal{E}'_{g_i}(t) = (\sum_{j=1}^{g-1} \mathcal{E}_j(t) \mathcal{E}_{g-j}(t)) +$
 257 $\mathcal{E}_{\frac{g}{2}}(t^2)$ and have $\mathcal{E}_g(t) = \frac{1}{2[1-\mathcal{U}(t)]} [\mathcal{E}'_{g_i}(t) + \mathcal{E}_{g_{\text{ii}}}(t) + \mathcal{E}_{g_{\text{iii}}}(t)]$. From eqs. 20-22, $\mathcal{E}_g(t)$ is a rational
 258 function in $\mathcal{U}(t)$ and $\mathcal{E}_\ell(t)$ for $1 \leq \ell \leq g-1$, as well as in $\mathcal{U}(t^2)$ and $\mathcal{E}_\ell(t^2)$ for $1 \leq \ell \leq g-1$.

259 **► Proposition 7.** *The generating function $\mathcal{E}_g(t)$ for the number of unlabeled galled trees with*
 260 *g galls satisfies as $t \rightarrow \rho^-$*

$$261 \quad \mathcal{E}_g(t) \sim \frac{\delta_g}{\gamma^{4g-1}(1-t/\rho)^{2g-1/2}}, \quad (23)$$

262 where δ_g is a constant dependent on g satisfying $\delta_1 = \frac{1}{2}$, and for $g \geq 2$,

$$263 \quad \delta_g = \frac{1}{2} \sum_{\ell=1}^{g-1} \left[\delta_\ell \delta_{g-\ell} + (\ell+1) \sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \delta_{d_j} \right]. \quad (24)$$

264 **Proof.** We proceed by induction. The claim holds for $g = 1$ (Proposition 1) and $g = 2$
 265 (eq. 15), with $\delta_2 = \frac{1}{2}[\frac{1}{2} \cdot \frac{1}{2} + 2 \cdot \frac{1}{2}] = \frac{5}{8}$. We assume inductively that for $\ell = 1, 2, \dots, g-1$,
 266 $\mathcal{E}_\ell(t) \sim \delta_\ell / [\gamma^{4\ell-1}(1-t/\rho)^{2\ell-1/2}]$, with constants δ_ℓ as in eq. 24. By the inductive hypothesis,
 267 the convergence radius of $\mathcal{E}_\ell(t)$ for each ℓ , $1 \leq \ell \leq g-1$, is ρ . Because $t^2 < t$ for $t < \rho$, $\mathcal{U}(t^2)$
 268 and $\mathcal{E}_\ell(t^2)$ can be treated as constants when finding the asymptotic behavior of $\mathcal{E}_g(t)$. As a
 269 result, using the inductive hypothesis, all terms in $\mathcal{E}_g(t)$ take the form $c / [\gamma^m(1-t/\rho)^{m/2}]$,
 270 and we must find the terms with the maximal power of $1/\sqrt{1-t/\rho}$.

271 We examine $\mathcal{E}'_{g_i}(t)$, $\mathcal{E}_{g_{\text{iii}}}(t)$, and then $\mathcal{E}_{g_{\text{ii}}}(t)$. By the inductive hypothesis,

$$\begin{aligned}
 272 \quad \mathcal{E}'_{g_i}(t) &\sim \sum_{j=1}^{g-1} \left[\frac{\delta_j}{\gamma^{4j-1}(1-t/\rho)^{2j-1/2}} \cdot \frac{\delta_{g-j}}{\gamma^{4(g-j)-1}(1-t/\rho)^{2(g-j)-1/2}} \right] \\
 273 \quad &\sim \sum_{j=1}^{g-1} \frac{\delta_j \delta_{g-j}}{\gamma^{4g-2}(1-t/\rho)^{2g-1}} \quad (25)
 \end{aligned}$$

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274

$$275 \quad \mathcal{E}_{g_{\text{iii}}}(t) \sim \sum_{\ell=0}^{\lfloor \frac{g-1}{2} \rfloor} \sum_{b=\ell}^{\lfloor \frac{g-1}{2} \rfloor} \left(\frac{1}{[1-\mathcal{U}(\rho^2)]^{\ell+1}} \sum_{\mathbf{d} \in C(b,\ell)} \prod_{j=1}^{\ell} \mathcal{E}_{d_j}(\rho^2) \right) \frac{\delta_{g-1-2b}}{\gamma^{4g-8b-5}(1-t/\rho)^{2g-4b-5/2}}. \quad (26)$$

276 Because the largest power of $1/(1-t/\rho)$ in $\mathcal{E}_{g_{\text{iii}}}(t)$ is less than $2g-1$, its largest power in
 277 $\mathcal{E}'_{g_i}(t)$, $\mathcal{E}_{g_{\text{iii}}}(t)$ does not affect the asymptotics of $\mathcal{E}_g(t)$.

278 For $\mathcal{E}_{g_{\text{ii}}}(t)$, for any $\ell = 1, 2, \dots, g-1$, two quantities determine the power of $1/\sqrt{1-t/\rho}$:
 279 both $\sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \mathcal{E}_{d_j}(t)$ and $[3\mathcal{U}(t) - 2 + \ell]/[1 - \mathcal{U}(t)]^{\ell+2} + \llbracket \ell = 1 \rrbracket$. First, according
 280 to the inductive hypothesis, for each ℓ , $1 \leq \ell \leq g-1$, noting $\sum_{j=1}^{\ell} d_j = g-1$,

$$281 \quad \sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \mathcal{E}_{d_j}(t) \sim \sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \frac{\delta_{d_j}}{\gamma^{4d_j-1}(1-t/\rho)^{2d_j-1/2}} \\ 282 \quad \sim \sum_{\mathbf{d} \in C(g-1,\ell)} \frac{\prod_{j=1}^{\ell} \delta_{d_j}}{\gamma^{4g-4-\ell}(1-t/\rho)^{2g-2-\ell/2}}. \quad (27)$$

283 Second, for ℓ , $1 \leq \ell \leq g-1$, from $\mathcal{U}(t) \sim 1 - \gamma\sqrt{1-t/\rho}$,

$$284 \quad \left(\frac{3\mathcal{U}(t) - 2 + \ell}{[1 - \mathcal{U}(t)]^{\ell+2}} + \llbracket \ell = 1 \rrbracket \right) \sim \frac{\ell + 1}{\gamma^{\ell+2}(1-t/\rho)^{(\ell+2)/2}}. \quad (28)$$

285 Combining eqs. 27 and 28, we obtain

$$286 \quad \mathcal{E}_{g_{\text{ii}}}(t) \sim \sum_{\ell=1}^{g-1} \sum_{\mathbf{d} \in C(g-1,\ell)} \frac{\prod_{j=1}^{\ell} \delta_{d_j}}{\gamma^{4g-4-\ell}(1-t/\rho)^{2g-2-\ell/2}} \cdot \frac{\ell + 1}{\gamma^{\ell+2}(1-t/\rho)^{(\ell+2)/2}} \\ 287 \quad \sim \sum_{\ell=1}^{g-1} \frac{(\ell + 1) \sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \delta_{d_j}}{\gamma^{4g-2}(1-t/\rho)^{2g-1}}. \quad (29)$$

288 The proof is concluded by noting

$$289 \quad \mathcal{E}_g(t) \sim \left[\sum_{j=1}^{g-1} \frac{\delta_j \delta_{g-j}}{\gamma^{4g-2}(1-t/\rho)^{2g-1}} + \sum_{\ell=1}^{g-1} \frac{(\ell + 1) \sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \delta_{d_j}}{\gamma^{4g-2}(1-t/\rho)^{2g-1}} \right] \frac{1}{2\gamma(1-t/\rho)^{1/2}} \\ 290 \quad \sim \frac{\sum_{\ell=1}^{g-1} [\delta_{\ell} \delta_{g-\ell} + (\ell + 1) \sum_{\mathbf{d} \in C(g-1,\ell)} \prod_{j=1}^{\ell} \delta_{d_j}]}{2\gamma^{4g-1}(1-t/\rho)^{2g-1/2}} \\ 291 \quad \sim \frac{\delta_g}{\gamma^{4g-1}(1-t/\rho)^{2g-1/2}}. \quad (30)$$

292

293 ► **Theorem 8.** *The asymptotic growth of the number $E_{n,g}$ of unlabeled galled trees with n*
 294 *leaves and a fixed number of galls $g \geq 1$ satisfies*

$$295 \quad E_{n,g} \sim \frac{\delta_g}{\gamma^{4g-1}\Gamma(2g - \frac{1}{2})} n^{2g-\frac{3}{2}} \rho^{-n} \sim \frac{2^{2g-1} \delta_g}{\gamma^{4g-1} (4g-3)!! \sqrt{\pi}} n^{2g-\frac{3}{2}} \rho^{-n}. \quad (31)$$

296 **Proof.** The first step follows from the transfer formula. For the second step of eq. 31, we
 297 recall $\Gamma(n + \frac{1}{2}) = [(2n-1)!!/2^n] \sqrt{\pi}$ with and $2g - \frac{1}{2} = (2g-1) + \frac{1}{2}$. ◀

298 The δ_g have a relationship with the Catalan numbers, $C_m = \binom{2m}{m}/(m+1)$.

299 ► **Proposition 9.** *The numbers $\{\delta_g\}_{g \geq 1}$ satisfy $2^{2g-1}\delta_g = C_{2g-1}$.*

300 **Proof.** We prove the result by showing that the generating function $\mathcal{D}(t) = \sum_{g \geq 1} 2^{2g-1}\delta_g t^{2g-1}$

301 is the odd part of the generating function of the Catalan numbers, $\mathcal{C}_O(t) = \sum_{g \geq 1} C_{2g-1} t^{2g-1}$.

302 $\mathcal{C}_O(t)$ satisfies $\mathcal{C}_O(t) = \frac{1}{2} \sum_{n \geq 0} [C_n t^n - C_n (-t)^n] = \sum_{n \geq 1} C_{2n-1} t^{2n-1}$, where $\mathcal{C}(t) =$

303 $(1 - \sqrt{1-4t})/(2t)$ is the generating function of the Catalan numbers. Hence, $\mathcal{C}_O(t) =$

304 $[1 - \frac{1}{2}(\sqrt{1-4t} + \sqrt{1+4t})]/(2t)$. From the recursion for δ_g (Proposition 7),

$$\begin{aligned}
 305 \quad \mathcal{D}(t) &= t + \sum_{g \geq 2} \left(\sum_{\ell=1}^{g-1} 2^{2g-2} \delta_\ell \delta_{g-\ell} \right) t^{2g-1} + \sum_{g \geq 2} \left[\sum_{\ell=1}^{g-1} (\ell+1) 2^{2g-2} \sum_{\mathbf{d} \in C(g-1, \ell)} \prod_{j=1}^{\ell} \delta_{d_j} \right] t^{2g-1} \\
 306 \quad &= t + \left[\sum_{\ell \geq 1} 2^{2\ell-1} \delta_\ell t^{2\ell-1} \sum_{g \geq \ell+1} 2^{2(g-\ell)-1} \delta_{g-\ell} t^{2(g-\ell)-1} \right] t \\
 307 \quad &+ \left[\sum_{\ell \geq 1} (\ell+1) (2t)^\ell \sum_{g \geq \ell+1} \sum_{\mathbf{d} \in C(g-1, \ell)} \prod_{j=1}^{\ell} 2^{2d_j-1} \delta_{d_j} t^{2d_j-1} \right] t \\
 308 \quad &= t + t\mathcal{D}^2(t) + t \sum_{\ell \geq 1} (\ell+1) [2t\mathcal{D}(t)]^\ell \\
 309 \quad &= t + t\mathcal{D}^2(t) + \frac{2t^2\mathcal{D}(t)}{[1-2t\mathcal{D}(t)]^2} + \frac{2t^2\mathcal{D}(t)}{1-2t\mathcal{D}(t)}. \tag{32}
 \end{aligned}$$

310 Solving for $\mathcal{D}(t)$, we obtain four solutions, only one of which has the correct limit of 0 as

311 $t \rightarrow 0$; this root is equal to $\mathcal{C}_O(t)$.

312 ◀

313 ► **Theorem 10.** *The number of unlabeled galled trees with n leaves and any fixed number of*

314 *galls $g \geq 0$ has asymptotic approximation*

$$315 \quad E_{n,g} \sim \frac{2^{2g-1}}{(2g)! \gamma^{4g-1} \sqrt{\pi}} n^{2g-\frac{3}{2}} \rho^{-n}. \tag{33}$$

Proof. The Catalan numbers satisfy $C_n = 2^n(2n-1)!/(n+1)!$, so that

$$\frac{2^{2g-1}\delta_g}{(4g-3)!!} = \frac{C_{2g-1}}{(4g-3)!!} = \frac{2^{2g-1}[2(2g-1)-1]!!}{(4g-3)!!(2g-1+1)!} = \frac{2^{2g-1}}{(2g)!}.$$

316 The case of $g = 0$ is included, as $E_{n,0} \sim [2^{-1}/(\gamma^{-1}\sqrt{\pi})]n^{-\frac{3}{2}}\rho^{-n} = [\gamma/2\sqrt{\pi}]n^{-\frac{3}{2}}\rho^{-n} \sim U_n$. ◀

317 Table 1 depicts the subexponential growth of $E_{n,g}$ for each g from 1 to 5. For $g = 1$ and

318 $g = 2$, the theorem recovers the values obtained in Propositions 2 and 5.

319 ► **Corollary 11.** *The exponential growth of the number $E_{n,g}$ of unlabeled trees with n leaves*

320 *and a fixed number of galls $g \geq 1$ is the same as that of U_n , the number of unlabeled trees with*

321 *no galls; however, the subexponential growth is greater by a factor of $4n^2/[\gamma^4(2g+1)(2g+2)]$.*

322 6 Discussion

323 We have studied the number of rooted binary unlabeled galled trees with a fixed number of

324 galls, analyzing the exponential growth of this quantity as the number of leaves increases.

325 We have found that the exponential growth, with the increase in the number of leaves n ,

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■ **Table 1** The subexponential portion $c_g n^{2g - \frac{3}{2}}$ of the growth $c_g n^{2g - \frac{3}{2}} \rho^{-n}$ with the number of leaves n of $E_{n,g}$, the number of galled trees with exactly g galls. Quantities are computed according to eq. 2 for $g = 0$ and Theorems 8 and 10 for $g \geq 1$.

Number of galls g	Exact constant c_g	Approximate value of c_g	$n^{2g - \frac{3}{2}}$
0	$\frac{\gamma}{2\sqrt{\pi}}$	0.3188	$n^{\frac{1}{2}}$
1	$\frac{1}{\gamma^3\sqrt{\pi}}$	0.3910	$n^{\frac{1}{2}}$
2	$\frac{5}{15\gamma^7\sqrt{\pi}} = \frac{8}{24\gamma^7\sqrt{\pi}} = \frac{1}{3\gamma^7\sqrt{\pi}}$	0.0799	$n^{\frac{5}{2}}$
3	$\frac{42}{945\gamma^{11}\sqrt{\pi}} = \frac{32}{720\gamma^{11}\sqrt{\pi}} = \frac{2}{45\gamma^{11}\sqrt{\pi}}$	0.0065	$n^{\frac{9}{2}}$
4	$\frac{429}{135135\gamma^{15}\sqrt{\pi}} = \frac{128}{40320\gamma^{15}\sqrt{\pi}} = \frac{1}{315\gamma^{15}\sqrt{\pi}}$	2.8638×10^{-4}	$n^{\frac{13}{2}}$
5	$\frac{4862}{34459425\gamma^{19}\sqrt{\pi}} = \frac{512}{3628800\gamma^{19}\sqrt{\pi}} = \frac{2}{14175\gamma^{19}\sqrt{\pi}}$	7.8062×10^{-6}	$n^{\frac{17}{2}}$

of the number of galled trees with a fixed number of galls is independent of the number of galls g (Corollary 11). This independence includes the case of $g = 0$ galls, the classic case of rooted binary unlabeled trees. It also implies that the number of galled trees whose number of galls is in some finite set G also has this same exponential growth.

The exponential growth with n of the number of galled trees with fixed g or with g in a finite set of values contrasts with the much greater increase in A_n , the number of galled trees with no restriction on the number of galls. This much larger growth for A_n is explained by the increase in the subexponential component with increasing g of the number of galled trees with n leaves and g galls, and the fact that with no maximum number of galls, as n increases, the number of terms in $A_n = \sum_{g \geq 0}^{\lfloor (n-1)/2 \rfloor} E_{n,g}$ grows without bound.

Our analysis produced a recursion for the Catalan numbers with odd indices: $C_{2n-1} = \sum_{m=1}^{n-1} C_{2m-1} C_{2(n-m)-1} + \sum_{m=1}^{n-1} (m+1)2^m \sum_{d \in C(n-1,m)} C_{2d_j-1}$. The first part comes from terms of $C_n = \sum_{m=0}^{n-1} C_m C_{(n-1)-m}$ with odd m and $(n-1) - m$; the second substitutes a sum involving Catalan numbers with odd index for terms with even m and $(n-1) - m$.

The difference across values of g in the growth of the number of trees with exactly $g \geq 0$ galls lies in the subexponential component, $c_g n^{2g - \frac{3}{2}}$. Related problems involving labeled phylogenetic networks show this same pattern, in which incrementing a constant associated with network complexity does change the subexponential growth but not the exponential growth. In particular, this pattern is seen with increasingly many reticulation nodes in various network classes [6, 7, 11, 12, 18]; the subexponential growth often includes a factor of n^2 , as in our case. Note additionally that beginning from $g = 1$, the constant c_g in the asymptotic approximation for $E_{n,g}$ decreases with g (eq. 31, Table 1). This property also holds for the labeled normal networks of Fuchs et al. [11, 12].

We comment that we could potentially have derived our generating functions by the symbolic method [10]. Our approach instead began with constructive enumeration of possible cases, using recursions to find the generating functions. The symbolic method potentially leads to simpler derivations that enable quick comparisons of relationships among enumerations for different types of galled trees.

By analyzing the asymptotics of $E_{n,g}$ for arbitrary g , this work solves unsolved problems from [1], who only analyzed $E_{n,1}$ and $A_n = \sum_{g \geq 0}^{\lfloor (n-1)/2 \rfloor} E_{n,g}$. The analysis has potential to assist in other scenarios with unlabeled phylogenetic networks indexed by a fixed quantity.

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