Distributions of cherries for two models of trees ☆

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Abstract

Null models for generating binary phylogenetic trees are useful for testing evolutionary hypotheses and reconstructing phylogenies. We consider two such null models – the Yule and uniform models – and in particular the induced distribution they generate on the number C_n of *cherries* in the tree, where a cherry is a pair of leaves each of which is adjacent to a common ancestor. By realizing the process of cherry formation in these two models by extended Polya urn models we show that C_n is asymptotically normal. We also give exact formulas for the mean and standard deviation of the C_n in these two models. This allows simple statistical tests for the Yule and uniform null hypotheses. © 2000 Elsevier Science Inc. All rights reserved.

Keywords: Trees; Phylogeny; Polya urn models; Yule model

1. Introduction

Phylogenetic trees are widely used in biology to represent evolutionary relationships between species. The shapes and branch lengths of such trees convey useful information regarding, for example, the rate of species formation and the occurrence of mass extinctions [1]. An unresolved debate concerns the relative importance of adaptive and stochastic factors in the process of lineage diversification. Adaptive factors are characteristics of a taxon thought to be responsible for the particular pattern of species survival or extinction observed in that taxon. Stochastic factors are those factors, random in appearance, that independently and uniformly effect the formation and extinction of all species in a tree.

Early stochastic modeling on phylogenetic trees concentrated on a qualitative comparison between actual phylogenetic trees and those produced in simulation studies [2,3]. While

suggestive, such work suffered from the lack of an explicit measure of the degree of similarity between actual and simulated trees. Later quantitative work, based on simple stochastic models of the process of species formation and extinction, introduced measures of similarity based on the frequency of tree topologies [4–6] and tree symmetry [7–10]. For a comprehensive review of past work see [11].

In this paper, we consider a simple and easily computed statistic for tree shape – namely the number of pairs of leaves that are adjacent to a common ancestor node – such a pair of leaves we will call a *cherry*. We will analyse the distribution of this statistic under the two simplest models for generating phylogenetic trees, namely the Yule model, and the uniform model. In particular, we give exact formulae for the mean and variance under both distributions, and show that this distribution is asymptotically normal as the number of leaves grows.

The structure of this paper is as follows. Section 2 reviews some basic terminology for phylogenetic binary trees. Following this, *extended Polya urn* models are described in Section 3. In Section 4 the Yule and uniform models are explained, and asymptotic normality results for the number of cherries are derived, along with exact formulae for the mean and variance. These results are used to develop statistical test for the Yule and uniform null hypotheses. The power of these tests is also calculated, using the other model as the alternative hypothesis. Section 5 concludes with a brief application to a 34-species tree.

2. Terminology

Evolutionary relationships are often represented by rooted or unrooted *binary (phylogenetic) trees* [12]. Such trees consist of labeled *nodes* of degree 1 called *leaves* and unlabeled *internal* nodes of degree 3 (also, in case the tree is rooted, it contains an additional *root node* of degree 2, so that every node can be regarded as having exactly two descendants). A pair of leaves adjacent to a common node is called a *cherry*. Edges adjacent to a leaf are called *pendant edges*, while all other edges are *internal*. A (tree) *shape* is the unlabeled tree obtained by dropping the labeling of the leaves of a binary phylogenetic tree. For further clarification of these terms see Fig. 1. The number
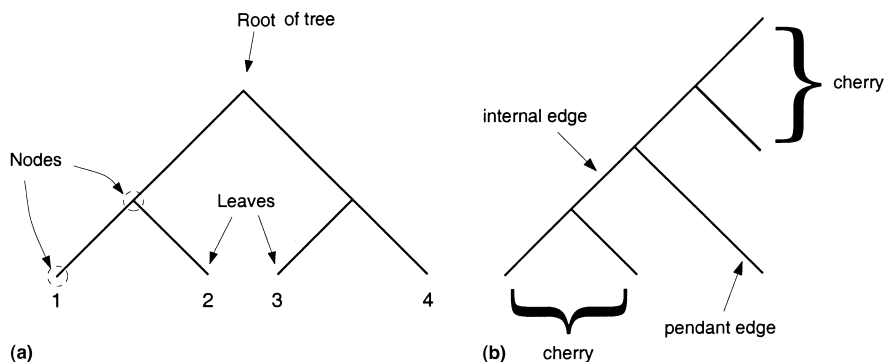

Fig. 1. Some terminology for trees: (a) a labeled rooted tree with four leaves; (b) an unrooted tree shape with five leaves.

of *rooted* leaf-labeled binary trees on n leaves is given by $(2n - 3)!! = 1 \times 3 \times 5 \times \cdots \times (2n - 3)$, and the number of *unrooted* leaf-labeled binary trees on n leaves is given by $(2n - 5)!! = 1 \times 3 \times 5 \times \cdots \times (2n - 5)$.

3. Extended polya urn (EPU) models

In this section, we review a recent central limit theorem concerning a general type of urn model, which will be useful for describing the asymptotic distribution of cherries.

Suppose an urn contains p types of balls. If a ball of the ith type ($i \in \{1, \ldots, p\}$) is drawn from the urn then it is returned, along with A_{ij} balls of the jth type. A_{ij} can be negative, this corresponding to the removal of balls from the urn. Models with $A_{ii} \geqslant 0$ (and commonly $A_{ij} \geqslant 0$) are referred to as *generalized polya urn* (GPU) models [13,14]. Allowing for A_{ii} to be negative, but requiring the number of balls returned each time to be a positive constant, defines the class of *extended polya urn* (EPU) models [15,16].

For both classes of urn models a number of asymptotic normality results exist, but in this paper we need only consider some specific asymptotic results for the EPU model, as follows [15,16].

Theorem 1 [15,16]. *Let $A = [A_{ij}]$ be the generating matrix for an EPU model, with principal eigenvalue λ_1. Let v be the left eigenvector of A corresponding to λ_1, where the entries v_i add up to one. Also let Z_{in} denote the number of balls of type i in the urn after n draws, where $i = 1, 2, \ldots, p$. For $p = 2$ suppose that*:
   (i) *A has constant row sums, where the constant is positive,*
   (ii) *λ_1 is positive, simple, and has a strictly positive left eigenvector v,*
   (iii) *$2\lambda < \lambda_1$ for the non-principal eigenvalue λ;*
then $n^{-1/2}(Z_{1n} - n\lambda_1 v_1)$ has asymptotically a normal distribution with mean of zero.
   Furthermore, for $p > 2$, suppose in addition:
   (iv) *$2\,Re(\lambda) < \lambda_1$ for all non-principal eigenvalues λ,*
   (v) *all complex eigenvalues are simple, and no two distinct complex eigenvalues have the same real part, except for conjugate pairs,*
   (vi) *all eigenvectors are linearly independent;*
then $n^{-1/2}(Z_{1n} - n\lambda_1 v_1, Z_{2n} - n\lambda_1 v_2, \ldots, Z_{(p-1)n} - n\lambda_1 v_{(p-1)})$ has asymptotically a joint normal distribution with mean of zero.

4. Probability distribution for cherries

4.1. Yule model

In the Yule model on rooted trees each pendant edge has an equal probability of splitting to form a cherry [17]. Equivalently an edge is added uniformly and randomly to a pendant edge at each step (Fig. 2). This model assumes that speciation is instantaneous, always occurs as bifurcations, and that the probability of speciation is the same for all lineages at any given time [18]. Extinction may be incorporated into this model by assuming that the probability of extinction is
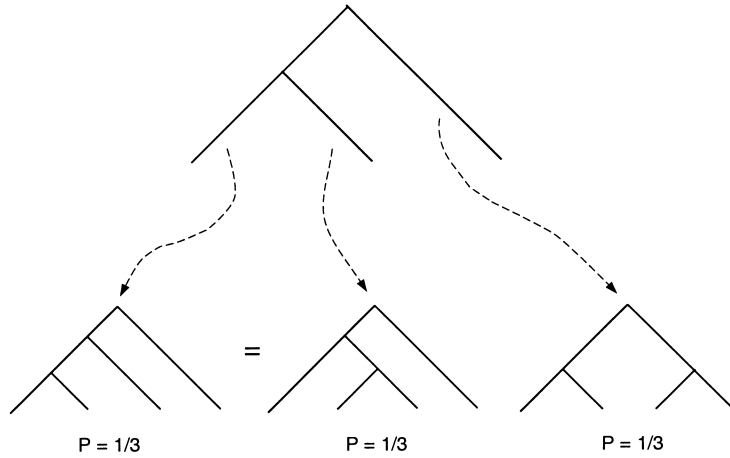
Fig. 2. The Yule model probabilities for shapes with four leaves. A shape on four leaves is formed by the splitting of one of the pendant edges of the shape on three leaves. Each pendant edge has the same probability of splitting, so for the shape on three leaves each pendant edge has a probability of $1/3$ of splitting. The resulting symmetric shape on four leaves has a probability of $1/3$. The other two shapes on four leaves are the same, and so the probability of this shape is $2/3$.

the same for all lineages, and independent across lineages. If this is the case then a Yule model can still be used, but with a different 'speciation' rate [5,19].

Theorem 2 [20]. *Let μ_n be the mean number of cherries for a rooted binary tree on n leaves, and σ_n^2 be the variance for the number of cherries. Under the Yule distribution we have the recursions, for $n \geqslant 2$:*

$$\mu_{n+1} = 1 + \mu_n\left(1 - \frac{2}{n}\right); \quad \sigma_{n+1}^2 = \sigma_n^2\left(1 - \frac{4}{n}\right) + \frac{2}{n}\mu_n\left(1 - \frac{2}{n}\mu_n\right)$$

which may be solved exactly to give

$$\mu_n = \frac{n}{3} \ (n \geqslant 3); \quad \sigma_n^2 = \frac{2n}{45} \quad (n \geqslant 5).$$

Proof. Let random variable C_n be the number of cherries on a rooted binary tree on n leaves. The proof relies on the following recursion for the probability generating function for C_n under the Yule model. Let $P_n(x) := \sum_{k \geqslant 2} \mathbb{P}[C_n = k]x^k$. Then, from Steel and Penny [20], we have the recursion, for $n \geqslant 4$:

$$P_{n+1}(x) = xP_n(x) + \frac{2x}{n}(1 - x)\frac{\mathrm{d}}{\mathrm{d}x}P_n(x), \tag{1}$$

and from this the recursions for the mean and variance follow directly by the usual techniques (noting that $\mu_n = \mathrm{d}/\mathrm{d}x\, P_n(x)|_{x=1}$ and $\sigma_n^2 = \mathrm{d}^2/\mathrm{d}x^2\, P_n(x)|_{x=1} + \mu_n - \mu_n^2$). The stated explicit formulas for the mean and variance can then be verified by induction on n. $\square$

The asymptotic probability distribution for the number of cherries in the Yule model may be found by realizing the process of cherry formation in an EPU model. Let the pendant edges that are part of a cherry be represented by black balls, and the rest of the pendant edges be represented by white balls. The number of cherries is then half the number of black balls, and the total number of pendant edges is equal to the number of black and white balls.

The following urn scheme generates a probability distribution for the number of black balls that is equal to the probability distribution for the number of pendant edges that are part of cherries. Starting with a rooted binary tree with two leaves, put two black balls into an empty urn. Select a ball at random from the urn, then return it. If the ball selected was black then put in a white ball. If the ball selected was white then put in two black balls, and take out a white ball. Repeat the process of random selection, and the addition or removal of balls $n - 2$ times, until there are n balls in the urn.

The generating matrix for this urn scheme is

$$A = \begin{pmatrix} 0 & 1 \\ 2 & -1 \end{pmatrix},$$

where balls of type one are black, and those of type two are white.

The eigenvalues of A are the principal eigenvalue $\lambda_1 = 1$, and $\lambda_2 = -2$. For the principal eigenvalue the left eigenvector, for which the entries add up to one, is $v = (2/3 \ 1/3)^{\mathrm{T}}$.

The conditions for the EPU model asymptotic results to apply in Theorem 1 are clearly satisfied so

$$\frac{1}{\sqrt{n}}(Z_{1n} - 2n/3) \to \mathcal{N}(0, c),$$

where $\mathcal{N}(\mu, \sigma^2)$ is a normal distribution with mean μ and variance σ^2.

Substituting $Z_{1n} = 2C_n$ gives

$$\frac{C_n - n/3}{\sqrt{cn/2}} \to \mathcal{N}(0, 1).$$

Using Theorem 2 the value of the constant c can be identified giving the following result.

Corollary 3. *For the Yule model on rooted trees*

$$\frac{C_n - n/3}{\sqrt{2n/45}} \to \mathcal{N}(0, 1).$$

4.2. Uniform model

In the uniform model on unrooted trees, equal probability is assigned to each possible leaf-labeled binary tree on n leaves. Alternatively, in the uniform model an edge is added uniformly and randomly to any edge at each step (Fig. 3). This process is not an explicit model of evolution, though a random sample of n species from a large group of species generated by a conditioned branching process follows a uniform distribution [21,22].
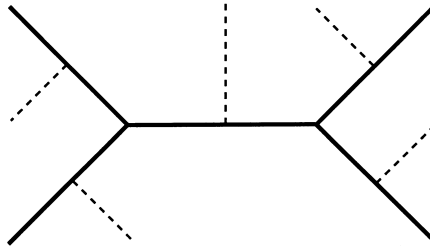
Fig. 3. The uniform model on unrooted trees. For the unrooted shape on four leaves (solid lines) there are five possible edges where the next edge (dashed lines) may be attached. The probability that the next edge will be attached to any particular one of the possible edges is 1/5.

Theorem 4 [20,23,24]. *Let μ_n be the mean for C_n for an unrooted binary tree on n leaves, and σ_n^2 be the variance for C_n. Under the uniform model, for $n \geqslant 4$,*

(a)

$$\mathbb{P}[C_n = k] = \frac{n!(n-2)!(n-4)!2^{n-2k}}{(n-2k)!(2n-4)!k!(k-2)!}, \quad k \geqslant 2.$$

(b)

$$\mu_n = \frac{n(n-1)}{2(2n-5)} \sim \frac{n}{4}; \quad \sigma_n^2 = \frac{n(n-1)(n-4)(n-5)}{2(2n-5)^2(2n-7)} \sim \frac{n}{16}.$$

Proof. Part (a) is due to Hendy and Penny [23], while the first part of (b) appears in Steel and Penny [20]. For the second (variance) part of (b) we note from Steel [24] that the pth cumulative moment of C_n is $((2(n-s)-5)!!n!)/(2^s(2n-5)!!(n-2s)!)$ (where the !! notation is as in Section 2) and thus,

$$\sigma_n^2 = \frac{n(n-1)(n-2)(n-3)}{2^2(2n-5)(2n-7)} + \mu_n - \mu_n^2.$$

Rearranging this last equation gives the result. □

The asymptotic probability distribution for the number of cherries in the uniform model may be found by an extension of the urn scheme for the Yule model. As before, let pendant edges that are part of cherries be represented by black balls and the other pendant edges by white balls. In addition, let the internal edges be represented by red balls.

The uniform model, with regard to the number of cherries, is equivalent to the following urn scheme. Starting with an unrooted binary tree with four leaves, put four black balls and one red ball into an empty urn. Select a ball at random from the urn, then return it. If the ball selected was black then put in a white ball and a red ball. If the ball selected was white then put in two black balls, take out a white ball, and put in a red ball. If the ball selected was red then put in a white ball and a red ball. Repeat the process of random selection, and the addition or removal of balls $n-4$ times, until there are n balls in the urn.

The generating matrix for this urn scheme is

$$A = \begin{pmatrix} 0 & 1 & 1 \\ 2 & -1 & 1 \\ 0 & 1 & 1 \end{pmatrix},$$

where balls of type one are black, type two are white, and type three are red.

The eigenvalues of A are $-2, 0$ and the principal eigenvalue of $\lambda_1 = 2$. For the principal eigenvalue the left eigenvector of A, for which the entries add up to one, is $v = (1/4 \ 1/4 \ 1/2)^T$. The conditions for the EPU model asymptotic results to apply in Theorem 1 are clearly satisfied so

$$\frac{1}{\sqrt{n}}(Z_{1n} - n/2) \to \mathcal{N}(0, c).$$

Substituting $Z_{1n} = 2C_n$ gives

$$\frac{C_n - n/4}{\sqrt{cn/4}} \to \mathcal{N}(0, 1).$$

Using Theorem 4 the value of the constant c can be identified, giving the following result.

Corollary 5. *For the uniform model on unrooted trees*

$$\frac{C_n - n/4}{\sqrt{n/16}} \to \mathcal{N}(0, 1).$$

4.3. Rooted and unrooted trees

The Yule and uniform models, as stochastic processes involving random edge addition, can apply to both rooted and unrooted trees. In the Yule model an edge is added uniformly and randomly to a pendant edge, while in the uniform model an edge is added uniformly and randomly to any edge (allowing a 'ghost' edge at the root in the rooted case). For the process of generating leaf-labeled trees two possible schemes are to add taxa in either fixed order or uniformly randomly. For the Yule model, the taxa must be added uniformly randomly in order to generate the correct probability distribution on leaf-labeled trees, while for the uniform model either scheme can be used.

We have so far only considered the cherry distribution for the Yule process on rooted trees and the uniform process on unrooted trees. How does the cherry distribution change if rooted trees are 'unrooted' by suppressing the root, or if unrooted trees are 'rooted' by the introduction of a root? A related question is what is the cherry distribution for the Yule process on *unrooted* trees, and the uniform process on *rooted* trees?

Consider firstly the unrooting of a rooted tree. Let T be a rooted tree on n leaves, with the number of cherries given by the random variable C_n. If the (degree 2) root of T is suppressed then the number of cherries (C_n^*) either remains the same, or increases by one; the latter occurs precisely when the tree shape has the generic shape shown in Fig. 4. Let $D_n = C_n^* - C_n \in \{0, 1\}$.

Lemma 6.
  (a) *For the Yule model on rooted trees*
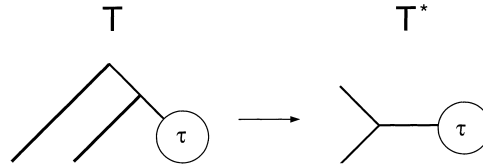 $$\lim_{n \to \infty} \mathbb{P}[D_n = 1] = 0.$$

Fig. 4. Rooted binary tree T for which the associated unrooted tree T^* has one more cherry. The tree T has n leaves, and the subtree τ has $n - 2$ leaves.

(b) *For the uniform model on rooted trees*

$$\lim_{n \to \infty} \mathbb{P}[D_n = 1] = 1/4.$$

Proof. D_n equals one precisely when the rooted tree shape is as shown in Fig. 4. For the Yule model, two applications of a recursive formula for tree probabilities [17] gives

$$\mathbb{P}[D_n = 1] = \frac{4}{(n-1)(n-2)} \sum_{\tau} \mathbb{P}[\tau] = \frac{4}{(n-1)(n-2)},$$

where the summation is over all subtree shapes τ on $n - 2$ leaves. Taking the limit gives the required result. For part (b), there are $(2n - 3)!!$ possible leaf-labeled rooted trees on n leaves. Of these $n(n - 1)(2n - 7)!!$ have the shape shown in Fig. 4. Therefore

$$\mathbb{P}[D_n = 1] = \frac{n(n-1)(2n-7)!}{(2n-3)!!} = \frac{n(n-1)}{(2n-3)(2n-5)},$$

and taking the limit gives the required result for the uniform model. $\quad\square$

If an unrooted tree is rooted, by subdividing some edge, then the number of cherries either remains the same or decreases by one; the latter occurs precisely when the tree is rooted on an edge that is part of a cherry. Since rooting or unrooting a tree changes the number of cherries by a maximum of one the asymptotic probability distribution for the number of cherries will remain unchanged.

Furthermore, the Yule and uniform processes can apply on both rooted and unrooted trees. For both processes the generating matrix for the corresponding EPU model is the same in the rooted and unrooted cases. Therefore, the asymptotic probability distribution for the number of cherries is the same for the rooted and unrooted versions of the Yule and uniform processes.

4.4. The Yule model null hypothesis

The Yule model can be used as a simple null hypothesis to explore patterns in phylogenetic trees. A simple two-tailed test of the Yule null hypothesis, for a given tree, can be made based on the number of cherries in the tree. If the number of cherries is below some lower critical value, or above some upper critical value, then the Yule null hypothesis is rejected. For small n, a recursive formula for the probabilities implicit in Eq. (1) may be used to calculate the rejection limits
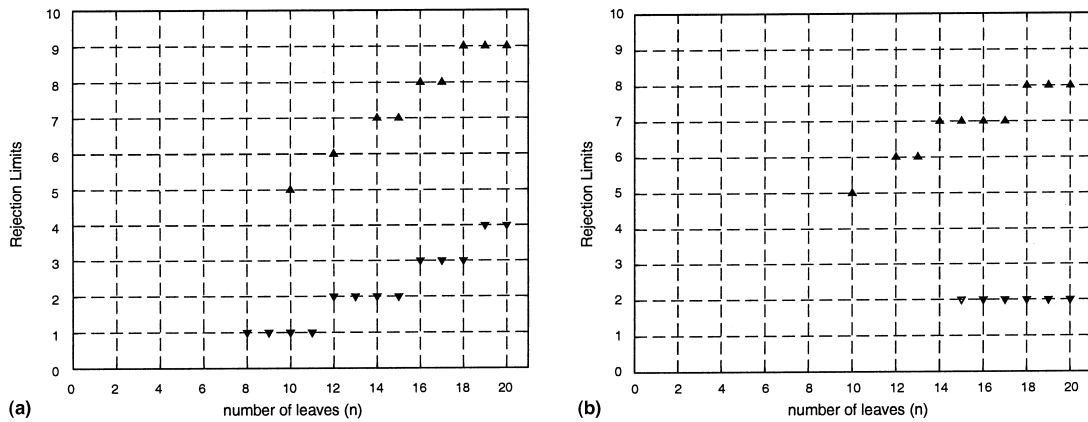
Fig. 5. Rejection limits for small n of the Yule and uniform null hypotheses at the $\alpha = 0.05$ level. Lower limits (▼) and upper limits (▲) were calculated from the exact probability distribution for the number of cherries. Where no triangle is shown the rejection limit does not exist. (a) Yule model; (b) uniform model.

(Fig. 5). For larger values of n ($n \gtrsim 20$) a normal approximation is valid. In this case, based on Corollary 3, the rejection region for a two-sided test at the α level is given by

$$C_n < \frac{n}{3} - Z_{\frac{\alpha}{2}}\sqrt{\frac{2n}{45}} \quad \text{and} \quad C_n > \frac{n}{3} + Z_{\frac{\alpha}{2}}\sqrt{\frac{2n}{45}}.$$

The lower and upper critical values for rejection at an $\alpha = 0.05$ level are shown in Fig. 6. If the Yule model is rejected then this implies that one or more of the assumptions upon which it is based is invalid. Often it is assumed that the assumption of equal probability of speciation is the invalid assumption, but this need not be the case [18].

4.5. Uniform model null hypothesis

In the uniform model, equal probability is assigned to each possible leaf-labeled binary tree on n leaves. Thus the uniform model distribution may be used to model the frequency of outcomes that would occur if the process of tree reconstruction did no better than random selection from the set of possible trees on n leaves. A test of the uniform model null hypothesis may be constructed based on the number of cherries in a tree. For small n the probability distribution given in Theorem 4 may be used to calculate the rejection limits (Fig. 5). For larger n ($n \gtrsim 20$) a analysis similar to that for the Yule model, but based on Corollary 5, gives as the rejection region:

$$C_n < \frac{n}{4} - Z_{\frac{\alpha}{2}}\sqrt{\frac{n}{16}} \quad \text{and} \quad C_n > \frac{n}{4} + Z_{\frac{\alpha}{2}}\sqrt{\frac{n}{16}}.$$

The lower and upper critical values for rejection at an $\alpha = 0.05$ level are shown in Fig. 6.
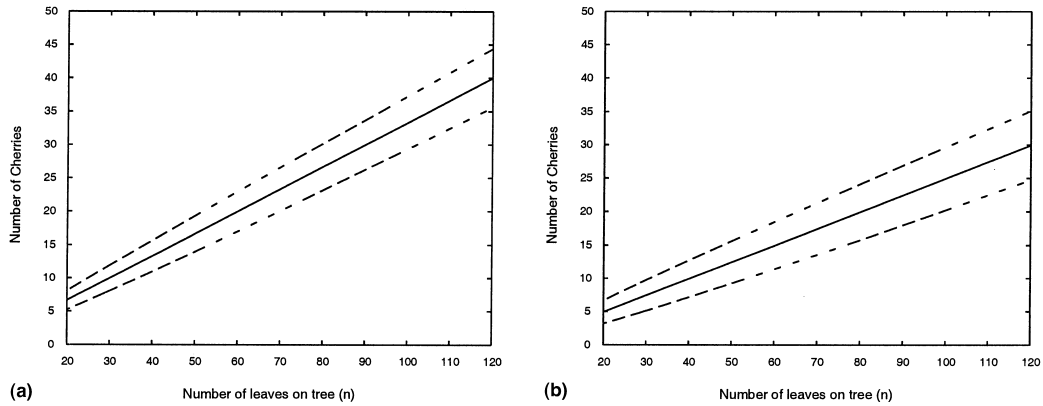
Fig. 6. Rejection limits for large n of the Yule and uniform null hypotheses at the $\alpha = 0.05$ level. The solid line represents the mean number of cherries, while the dashed lines are the lower and upper limits for rejection of the null hypotheses. The rejection limits are based upon a normal approximation which is valid for $n \gtrsim 20$. (a) Yule model; (b) uniform model.

4.6. Power of tests

The *power* of a test is the probability that the null hypothesis will be rejected given that the alternative hypothesis is true. Calculating the power of the test for the Yule null hypothesis against the uniform model alternative hypothesis gives

$$\text{power}(n) = \mathbb{P}\left[Z < \sqrt{n}/3 - r_1\right] + \mathbb{P}\left[Z > \sqrt{n}/3 + r_1\right], \qquad r_1 = 4\sqrt{\frac{2}{45}}Z_{\frac{\alpha}{2}}.$$

Similarly, the power of the test for the uniform model null hypothesis may be calculated against the alternative hypothesis that the Yule model is true to give

$$\text{power}(n) = \mathbb{P}\left[Z < -\frac{1}{4}\sqrt{\frac{5}{2}}\sqrt{n} - r_2\right] + \mathbb{P}\left[Z > -\frac{1}{4}\sqrt{\frac{5}{2}}\sqrt{n} + r_2\right], \qquad r_2 = \frac{1}{4}\sqrt{\frac{45}{2}}Z_{\frac{\alpha}{2}}.$$

Plotting the power, as a function of n, shows that in both cases the number of leaves must exceed 80 before the power of the tests rises above 0.9 (Fig. 7). So, unless one is dealing with large trees, the tests lacks the power to distinguish between the two models.

5. An example

Fig. 1 in [25] is a rooted phylogenetic tree for 34 species of *Eureptantic nemerteans* (ribbon worms). This tree has seven cherries (rooted or unrooted). For the Yule model null hypothesis test at the $\alpha = 0.05$ level the lower rejection limit is eight cherries or less, and the upper rejection limit is 15 cherries or more. So for the ribbon worm tree the Yule model null hypothesis is rejected. For the uniform model null hypothesis test at the $\alpha = 0.05$ level the lower rejection limit is five cherries or less, and the upper rejection limit is 13 cherries or more, and so the test does not reject the
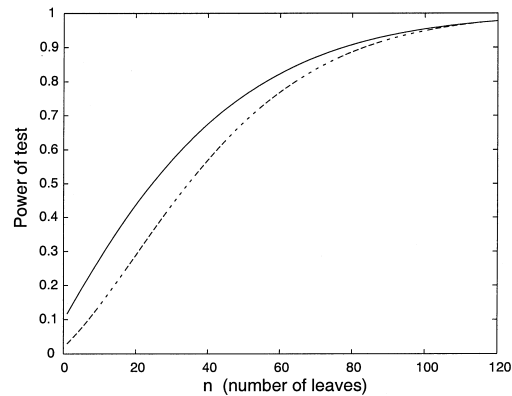
Fig. 7. The power of the tests for the Yule and uniform models. The solid line is the power of the test for the Yule model null hypothesis against the uniform model alternative. The dashed line is the power of the test for the uniform model null hypothesis test against the Yule model alternative.

uniform model null hypothesis. In any hypothesis test, however, it is important to note that a reconstructed tree is only an estimate of the underlying species tree. Consequently a more refined analysis would take into account the uncertainty and possible biases in phylogeny reconstruction [11,26].

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