

The Yule model

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22. May, 2007

1 Probability density for Yule model

The Yule model of branching is a pure birth process in which each branch has associated with it a birth rate (λ) determining the instantaneous rate at which the branch gives birth to a new branch (bifurcates into two branches). Starting at the root of a tree (the first bifurcation), there are two descendant branches, each with a birth rate of λ . This gives rise to the following probability density function for the time to the second bifurcation (t_2):

$$p(t_2|\lambda) = 2\lambda e^{-2\lambda t_2} \quad (1)$$

This is simply an exponential distribution with a mean of $\frac{1}{2\lambda}$. Likewise the probability density for the time from the $(i-1)$ th to the i th bifurcation (t_i) is:

$$p(t_i|\lambda) = i\lambda e^{-i\lambda t_i} \quad (2)$$

So the probability density for a tree that has *just reached* the n th bifurcation is:

$$q(\mathbf{t}|\lambda, n) = \prod_{i=2}^{n-1} i\lambda e^{-i\lambda t_i} \quad (3)$$

However most trees are not sampled exactly at the moment of the final bifurcation event. This means there is a final time t_n over which *none* of the n branches bifurcated. The probability of waiting t_n time without seeing any of the n branches bifurcate is $e^{-n\lambda t_n}$ giving rise to a total probability of a tree of n tips:

$$p(\mathbf{t}|\lambda, n) = (n-1)!\lambda^{n-2} \prod_{i=2}^n e^{-i\lambda t_i} \quad (4)$$

Remembering that $e^a e^b = e^{a+b}$ and defining the total tree length $s = \sum_{i=2}^n i t_i$ we have:

$$p(\mathbf{t}|\lambda, n) = (n-1)!\lambda^{n-2} e^{-\lambda s} \quad (5)$$

This probability density is the same as that of equation (3) in Nee *et al* (2001), despite Nee making the confusing assertion that his equation (3) is conditional on the root height. From the construction above, it is clear that no such conditioning exists.

2 Expectation of the tree height and total tree length under the Yule model

Defining the total tree height, $t_{MRC A} = \sum_{i=2}^n t_i$, it is easy to show that the expected tree height is:

$$E(t_{MRC A}) = \sum_{i=2}^n \frac{1}{i\lambda} \quad (6)$$

So for a 4 taxon tree and $\lambda = 2$ the expected height is:

$$E(t_{MRC A}) = \frac{1}{4} + \frac{1}{6} + \frac{1}{8} = 0.5416666 \quad (7)$$

The total expected tree length (s) of a Yule branching process is:

$$E(s) = \sum_{i=2}^n \frac{1}{\lambda} = \frac{n-1}{\lambda} \quad (8)$$

So for a 4 taxon tree and $\lambda = 2$ the expected height is:

$$E(s) = \frac{3}{2.0} = 1.5 \quad (9)$$