

Methods to estimate extinction and speciation rates, and shifts in those rates, from a phylogeny

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Annotated Bibliography

Papers that have tested for shifts in diversification rates:

Wiegmann, B. M., C. Mitter and B. Farrell. 1993. Diversification of carnivorous parasitic insects: Extraordinary radiation or specialized dead end? *The American Naturalist* 142:737–754.

Sister group comparisons, using a sign test, and a Wilcoxon signed-rank test. I thought this paper was significant for a methodological advance, but on skimming it, it didn't seem so.

Hodges, S. A. and M. L. Arnold. 1995. Spurring plant diversification: Are floral nectar spurs a key innovation? *Proceedings: Biological Sciences* 262:343-348.

Do two things – for the *Aquilegia* dataset, they use Sanderson and Donoghue's three-taxon ML approach (1994). And then they do a lit review of sister groups comparisons, with Wilcoxon signed-rank test, and "Fisher's Combined Probability Test" (see Slowinski & Guyer 1993). They have a graphical representation of the models of the Sanderson and Donoghue test, which is interesting.

Barracough, T. G., P. H. Harvey and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London B* 259:211-215.

Sister group comparisons, with a sign test. Also a randomization test (which they don't describe, instead referring the reader to Siegel 1956).

Hodges, S. 1997. Floral nectar spurs and diversification. *Int. J Plant Sci.* 158:81-88.

More a review, than anything. Includes good stuff on the ecology/mechanism of why flora spurs might be a key innovation. Basic methods – sister group comparisons. Unless you're interested in nectar spurs, read the 1995 paper instead.

McPeck, Mark A. 2008. The ecological dynamics of clade diversification and community assembly. *Am Nat* 172:E270-E284.

This one's for Dudu! He takes the ecological perspective—that diversification rates should slow as ecological niches are filled. Uses Pybus and Harvey's (2000) gamma statistic for his test. And then proposes an elaborate metacommunity model, which I'd have to reread several times to maybe-understand.

Papers more focused on methods/models:

Mitter, C., B. D. Farrell and B. Wiegmann. 1988. The phylogenetic study of adaptive zones: Has phytophagy promoted insect diversity? *The American Naturalist* 132:107-128.

Seems like a reasonable starting point (time-wise). They're focused on the relationship between diversification and particular traits ("key innovation" hypotheses), and set the scene by emphasizing the need to move past post-hoc explanations ("there are lots of insects, insects can fly, so flight was probably important for their macroevolutionary success"). They advocate sister-group comparisons, and while they cite others who have done the same ("Hennig 1966; Cracraft 1982; Eldredge 1982; Novacek and Norell 1982; Mitter and Brooks 1983; Larson 1985"), theirs is the first systematic approach I've seen. They use a sign test.

Slowinski, J. B. and C. Guyer. 1989. Testing the stochasticity of patterns of organismal diversity: An improved null model. *The American Naturalist* 134:907-921.

In comparison with Mitter et al., this paper is perhaps the first of the non trait-related approaches. They seek to develop a null model for tree shape, against which actual trees can be compared, agnostic of any associated traits (linking traits to those anomalous areas of trees would be done post-hoc). They are thus in the tradition of the “Woods Hole” paleontologists who sought null models for diversification patterns (e.g., “Raup et al. 1973, Raup & Gould 1974, Schopf et al. 1975, Gould et al. 1977, Raup 1977”), prior to resorting to adaptive explanations. They use a Yule model for their null, and ask for the node in question, what is the probability of getting a split at least this extreme? They can thus do their test on a single tree (multiple comparisons are not necessary). And a good reminder that they were writing in the 80s when they refer to large phylogenies as those with more than seven tips.

Heard, S. B. 1992. Patterns in tree balance among cladistic, phenetic, and randomly generated phylogenetic trees. *Evolution* 46:1818-1826.

A response to the early concern that different tree estimation methods had different biases with respect to the tree shapes they tended to produce. “In contrast to previous suggestions, I find cladistic trees to be no more imbalanced than phenetic trees when confounding variables are appropriately controlled. The degree of imbalance found in literature trees is inconsistent with the uniform-rate speciation model; this is most likely a result of variability in speciation and extinction rates among real lineages” (abstract).

Nee, S., A. O. Mooers and P. H. Harvey. 1992. Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences of the United States of America* 89:8322-8326.

Single-tree work. Perhaps the first robust use of lineage-through-time plots, and the first look at density-dependent diversification? Focus on the Sibley-Ahlquist bird data for the first bit, and then seem to dance around about with other datasets. From the abstract: “The analysis of the tempo and mode of evolution has a strong tradition in paleontology. Recent advances in molecular phylogenetic reconstruction make it possible to complement this work by using data from extant species.”

Hey, J. 1992. Using phylogenetic trees to study speciation and extinction. *Evolution* 46:627-640.

Similar to the above? Lots of math. Too burned to understand. Null models, null models, null models. Apparently (among the?) first study to evaluate a Moran model—one where diversity does not increase indefinitely, but rather reaches a ceiling, after which $b=d$ (a lineage has to go extinct before a new one can diversify).

Sanderson, M. J. and G. Bharathan. 1993. Does cladistic information affect inferences about branching rates? *Systematic Biology* 42:1-17.

Takes a different perspective, because they are interested in the rate values themselves, not merely in the relative rates between different clades.

Slowinski, J. B. and C. Guyer. 1993. Testing whether certain traits have caused amplified diversification: An improved method based on a model of random speciation and extinction. *The American Naturalist* 142:1019-1024.

Critique the Mitter et al. repeated-sister-group-comparisons school, for two main reasons. First, they “biased their results by choosing traits to test that they knew to be associated with diverse groups, a practice that introduces problems with Type I statistical error ... Ideally, traits should be chosen in ignorance of the diversity of the groups possessing them and because there are theoretical reasons to believe that they would cause amplified diversification” (1021). And second, their reduction of the sister-group comparisons to a simple sign test removed much of the power. So they (Slowinski & Guyer) bring in their 1989 Yule null model, and advocate for summing the probabilities of split imbalances using “Fisher's combined probability test.”

Sanderson, M. J. and M. J. Donoghue. 1994. Shifts in diversification rate with the origin of angiosperms. *Science* 264:1590-1593.

Among other things, this paper introduced a three-taxon ML approach to testing for the correlation between the evolution of a trait, and an increase in rates of diversification. I didn't cover it in my overview because it was an awkward fit in my organizational scheme, and because I didn't understand it well enough. I think we've moved beyond...

Nee, S., E. C. Holmes, R. M. May and P. H. Harvey. 1994. Extinction rates can be estimated from molecular phylogenies. *Philosophical Transactions of the Royal Society of London B* 344:77-82.

Good insight: assuming a constant birth/death model, you get a linear lineage-through-time plot, and the upswing at the end gives you the birth rate, so you can calculate the death rate.

Nee, S., R. M. May and P. H. Harvey. 1994. The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society B: Biological Sciences* 344:305-311.

Math! Ack. Generalize birth/death models to account for the inclusion of only extant taxa in phylogenies, and additionally for the effects of incomplete sampling. And then how to infer birth and death rates. Important equations referenced, for example, in the BiSSE paper.

Harvey, P. H., R. M. May and S. Nee. 1994. Phylogenies without fossils. *Evolution* 48:523-529.

More detailed work on birth-death models, and lineage-through-time plots. An interesting new contribution is the observation (through simulation) that mass extinctions leave a signal in phylogenies build of only extant taxa.

Kubo, T. and Y. Iwasa. 1995. Inferring the rates of branching and extinction from molecular phylogenies. *Evolution* 49:694-704.

This is a trait-free examination (the whole tree is inspected for "signatures" of macroevolutionary events/trends). Uses a constant-rate birth-death model. They are perhaps the first to note that branching rates are much more easily estimated than are extinction rates, which they find to be plagued by high variance and bias.

Purvis, A., S. Nee and P. H. Harvey. 1995. Macroevolutionary inferences from primate phylogeny. *Proceedings: Biological Sciences* 260:329-333.

Came to this paper late in this exercise, somehow, but it looks like a goodie. What you can do when you have a complete phylogeny... They used a birth-death model, and compared the departures of clades from the global ML estimates using LRTs, etc. Basically, a manual MEDUSA that requires fully resolved clades? Also test models of density-dependent cladogenesis.

Paradis, E. 1997. Assessing temporal variations in diversification rates from phylogenies: Estimation and hypothesis testing. *Proceedings of the Royal Society B: Biological Sciences* 264:1141-1147.

Nee (2001) reports that this paper includes a faulty likelihood function.

Paradis, E. 1998. Detecting shifts in diversification rates without fossils. *Am Nat* 152:176-187.

"The idea proposed here is to analyze divergence times of a group of species as estimated from a phylogenetic tree with the statistical models used to analyze survival data" (177). "One of the main advantages of the method reported here compared to others is that full use of the available phylogenetic information is made: not only the divergences that are precisely dated but also those that are unknown, provided that an interval for their age can be estimated" (183). If I understand correctly, one of the few genuine departures from a birth-death model for this sort of work. They've been critiqued for assuming that there is no extinction.

Pybus, O. and P. Harvey. 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B: Biological Sciences* 267:2267.

Test against the null model of constant extinction and speciation rates throughout a phylogeny. Not explicitly trait oriented—agnostic at first, and then one could inspect for correlations. Make the point that birth-death models allow for two classes of investigation (and provide good references of each):

1) Do extinction and/or speciation rates vary between lineages? And 2) If they don't, what are those rates, and are they constant through time? Their paper is devoted to the latter question, and they point to the lack of a coherent model that is capable of accounting for both types of variation. They have a nice brief review of the limiting assumptions of some of the earlier models, and put on a lot of emphasis on the robustness of their own approach to incomplete sampling. They introduce a "gamma" statistic that is a reflection of the distribution of nodes in a tree (with respect to their proximity to the root or tips): "Consider a complete reconstructed phylogeny that is the result of a constant-rates birth-death process with parameters b and d . If d is large then the phylogeny's internal nodes will tend to occur near its tips ... because lineages that arose in the recent past are less likely to be removed by extinction than lineages that arose in the distant past. The strength of the pull depends on d/b , and increases as d/b increases (Nee et al. 1994a). Therefore, we might expect that the internal nodes of the phylogeny are, on average, closest to the root when $d/b=0$ (the pure birth model)" (2268).

Magallón, S. and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. *Evolution* 55:1762-1780.

This is an interesting paper, in the trait-free, constant-rates camp. They use a time-continuous birth-death model, and estimate the relevant parameters from a fossil-calibrated tree of the angiosperms (thus explicitly time-based, but focused only on clade ages, not on distributions of branchlengths, so they can't estimate extinction rate individual. Instead they do their study first with very low extinction, and then very high extinction, to be conservative). And then look for clades outside the 95% confidence intervals for these parameters—they are thus a direct precursor to the MEDUSA-type analyses.

Nee, S. 2001. Inferring speciation rates from phylogenies. *Evolution* 55:661-668.

Math-heavy exploration of the different ways proposed to estimate speciation rates from phylogenies (including Paradis, Hey). Some interesting stuff on subtle difference in models, and the effect those differences have on calculating the maximum likelihood estimator and confidence interval for each model (663). Lots about calculating confidence intervals for the estimates of speciation rate. Why I'm out of my league: "Arguably the simplest model, there nonetheless exists, at the very least, six different ways to derive a confidence interval for the speciation rate of a clade using [the Yule model] and the likelihood approach to statistical inference" (661).

Agapow, P.-M. and A. Purvis. 2002. Power of eight tree shape statistics to detect nonrandom diversification: A comparison by simulation of two models of cladogenesis. *Systematic Biology* 51:866.

Focused on treeshape, only—no branchlengths. As far as I can tell. And then a power analyses for various metrics, using somewhat odd models (one declining with time since speciation, the other associated with a trait). Old-school. But, see Chan & Moore...

Chan, K. M. A. and B. R. Moore. 2002. Whole-tree methods for detecting differential diversification rates. *Systematic Biology* 51:855-865.

This paper introduces a series of topology-based indices for whole-tree, trait-agnostic, detection of diversification patterns that differ significantly from the null expectation. Has an excellent introduction to diversification methods, with a very handy division of approaches into temporal vs. topological (theirs is topological), and the topological approaches further into single node vs. tree-shape indices. See also Chan & Moore 2005 (software).

Bokma, F. 2003. Testing for equal rates of cladogenesis in diverse taxa. *Evolution* 57:2469-2474.

This is a tree-free approach, requiring only a clade's richness and its age, "based on the assumption that speciation and extinction probabilities have been constant over time and across lineages." Uses ML estimation of the parameter values for each clade, and then compares them (likelihood ratio test, I believe). I don't understand how they get extinction rates from an unresolved topology.

Ree, R. H. 2005. Detecting the historical signature of key innovations using stochastic models of character evolution and cladogenesis. *Evolution* 59:257-265.

A key innovation test (i.e., trait-dependent). Instead of using clade size, it uses "waiting times" – ie the rate of divergences. Thus it is sensitive to branch length info, rather than just to distribution of the character state on the tips.

Rabosky, D. L., S. Donnellan, A. Talaba and I. Lovette. 2007. Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society B* 274:2915.

Another case of somehow using a birth-death model on an unresolved phylogeny. Citing a lot of Sanderson's work for the math, which I didn't follow. They look for shifts in diversification rate in a way very analogous to MEDUSA (but manually).

Maddison, W. 2006. Confounding asymmetries in evolutionary diversification and character change. *Evolution* 60:1743–1746.

Critical insight, in my humble opinion. Biases in state transitions (more likely to go from state x to state y than the other way around) and biases in diversification rates (lineages in state x more likely to diversify than are lineages in state y) are confounded, and should not be estimated separately. Provides the theoretical motivation for BiSSE (Maddison et al. 2007).

Rabosky, D. L. and I. Lovette. 2008. Explosive evolutionary radiations: Decreasing speciation or increasing extinction through time? *Evolution* 62:1866-1875.

Not sure how to reconcile this paper with his later comment (Rabosky 2009b) that extinction should not be estimated from molecular phylogenies. "Here we develop a method for estimating speciation and extinction rates that vary continuously through time. By applying this approach to real phylogenies with explosive-early diversification and by modeling features of lineage-accumulation curves under both declining speciation and increasing extinction scenarios, we show that a signal of explosive-early diversification in phylogenies of extant taxa cannot result from increasing extinction and can only be explained by temporally declining speciation rates. Moreover, whenever extinction rates are high, "explosive early" patterns become unobservable, because high extinction quickly erases the signature of even large declines in speciation rates" (abstract).

Bokma, F. 2008. Bayesian estimation of speciation and extinction probabilities from (in)complete phylogenies *Evolution* 62:2441-2445.

No entiendo. "However, due to different estimation techniques, estimates from complete and incomplete phylogenies are difficult to compare statistically. Here I show with some examples how existing likelihood functions can be used to obtain Bayesian estimates of speciation and extinction probabilities, and how this approach is applied to both complete and incomplete phylogenies."

Software

Chan, K.M.A and B. Moore. 2005. SymmeTREE: Whole-tree analysis of differential diversification rates. *Bioinformatics* 21:1709.

See their 2002 paper for the theory.

Rabosky, D. 2006. LASER: A maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evolutionary Bioinformatics Online* 2:273.

“LASER is a package for the R programming environment that implements maximum likelihood methods based on the birth-death process to test whether diversification rates have changed over time. LASER contrasts the likelihood of phylogenetic data under models where diversification rates have changed over time to alternative models where rates have remained constant over time” (abstract). It seems that this package has been subsumed into MEDUSA.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor and W. Challenger. 2007. GEIGER: Investigating evolutionary radiations. *Bioinformatics* 24:129-131.

An R package that incorporates lots of stuff—character evolution, tree simulation, hypothesis tests—including the estimation of diversification-related parameters, and the testing of diversification-related hypotheses.

Maddison, W. P., P. E. Midford and S. P. Otto. 2007. Estimating a binary character's effect on speciation and extinction. *Systematic Biology* 56:701-710.

Great paper. BiSSE. See also Maddison 2006, and Fitzjohn et al. 2009.

Bokma, F. 2008. Detection of "punctuated equilibrium" by Bayesian estimation of speciation and extinction rates, ancestral character states, and rates of anagenetic and cladogenetic evolution on a molecular phylogeny. *Evolution* 62:2718-2726.

No entiendo. Software is available as a Matlab file.

Alfaro, M. E., F. Santini, C. Brock, H. Alamillo, A. Dornburg, D. L. Rabosky, G. Carnevale and L. J. Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* 106:13410-13414.

The introduction to MEDUSA. Takes a large tree (unresolved clades are fine, as long as their richness is known), and fits a birth-death model to it, with b and d optimized by ML. Then choose a branch on which to allow a new b and d , computes the likelihood, and accepts or rejects based on the AIC (with the new b and new d counting as parameters, plus one for the breakpoint). More or less. Then some nuances about former breakpoints, etc. Again, I'm confused about how they estimate death rates from largely unresolved trees.

FitzJohn, R. G., W. Maddison and S. P. Otto. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology* 58:595–611.

A modification of BiSSE to account for incomplete sampling, and incomplete resolution. See Maddison et al. 2007.

Reviews and Reviewish Things

Purvis, A. 1996. Testing macroevolutionary hypotheses. In *New uses for new phylogenies* (ed. P.H. Harvey, A.J. Leigh Brown, J. Maynard Smith, S. Nee), pp. 153–168. Oxford University Press.

Haven't read this. But it sounded important. "New phylogenies," even!

Sanderson, M. J. and M. J. Donoghue. 1996. Reconstructing shifts in diversification rates on phylogenetic trees. *TREE* 11:15-20.

Much of this review is devoted to estimates of absolute rates, and then shifts in those rates. (Rather than, for example, demonstrating a correlation between rate and trait).

Mooers, A. and S. B. Heard. 1997. Inferring evolutionary process from phylogenetic tree shape. *Quarterly Review of Biology* 72:31-54.

A good review on tree shape, indices of tree balance, and the use of null models for tree shape in the testing of macroevolutionary questions. Includes discussion of lineage-through-time plots, etc.

De Queiroz, A. 1998. Interpreting sister-group tests of key innovation hypotheses. *Systematic Biology* 47:710–718.

A good critique of much of the 1990s' approaches to testing trait-linked diversification hypotheses. Main points are the invalidity (he argues) of the constant-rate birth-death model as a biological reasonable null, and issues of causation and correlation. He ultimately comes out tentatively in favour of the sign test over all others, drawing a distinction between "tests based on counting," and those "based on magnitude," and arguing that the former, while less powerful, are more likely to capture genuine correlations.

Aldous, D. 2001. Stochastic models and descriptive statistics for phylogenetic trees, from Yule to today. *Statistical Science* 16:23-34.

It's a chat with a statistician about tree-imbalance! Nice historical review. Among the last papers to focus mostly on treeshape as topology only (ignoring branchlengths, but see, e.g., Chan & Moore). Claims that, when only topology is considered, treeshape is uninformative about evolutionary process: "While this observation is not new (see, e.g., Slowinski and Guyer, 1989), its implications have, in my view, been insufficiently emphasized in the biological literature. One is studying what tree shape says about macroevolution; macroevolution is driven by speciations and extinctions; so one might take for granted that tree shape has some relation to overall rates of speciation and extinction. But it does not. That is, within model (*) ... the shape of the cladogram on extant species is unaffected by (and hence tells us nothing about) past overall rates of speciation and extinction" (30).

Concludes that tree imbalance in real data is stronger than expected under our models, and we still don't know why.

Barracough, T. G. and S. Nee. 2001. Phylogenetics and speciation. *TREE* 16:391-399.

Didn't reread, but thought it was good the first time...

Nee, S. 2006. Birth-death models in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* 37:1–17.

"Birth-death models have a distinguished and continuing history in macroevolutionary inference. Occasionally, improved models are recommended. These are usually premised on the idea that more realistic models are to be preferred or that a model that better fits observed patterns is a step forward. In my opinion, there is no substitute for models that have a simple interpretation and lead to easy inference, and whose failure is often of more interest than the ability to fit an observed pattern. I expect the sort of models discussed here to maintain their pre-eminence for a long time to come" (14).

Rabosky, D. 2006. Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 60:1152-1164.

"Here I examine model selection, parameter estimation, and power to reject the null hypothesis using likelihood models based on the birthdeath process."

Ricklefs, R. 2007. Estimating diversification rates from phylogenetic information. *TREE* 22:601-610.

Good stuff. Pretty pictures. And a decent (although bird-heavy) sample of lit for papers that have used the various approaches.

Is this true?? "Individual branch lengths in a reconstructed phylogeny estimate the inverse of the diversification rate $[1/(l - m)]$, on average, deep in the phylogeny, and the inverse of the speciation rate $(1/l)$ toward the present. **Each branch length is statistically independent**, and so one can use a sample of branch lengths from one or more phylogenetic trees to estimate rates of diversification" (607).

Misc:

Revell, L. J., L. J. Harmon and R. E. Glor. 2005. Underparameterized model of sequence evolution leads to bias in the estimation of diversification rates from molecular phylogenies. *Syst. Biology* 54:973-983.

Issue a general critique of methods that are contingent on branchlengths, by showing that while topology estimates are general robust to model underparameterization, branchlengths aren't. So failure to account for heterogeneity in rates of molecular evolution across sites (for example) can have strong effects on diversification tests based on branchlengths.

Bokma, F. 2009. Problems detecting density-dependent diversification on phylogenies. *Proceedings of the Royal Society B: Biological Sciences* 276:993-994.

This is a comment on the Rabosky and Lovette woodwarbler paper—basically critiques them for making inference about speciation rates using the number of taxa present in their phylogeny at a given point, rather than the number of species present in nature at that point (ie, ignoring extinction). Density-dependent wars (see McPeck 2008).

Rabosky, D. L. 2009. Ecological limits and diversification rate: Alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters* 12:735-743.

Argues for a union of evolution and ecology, specifically that it is unreasonable to assume that diversification rates should remain constant through time—there should be a ecological effect of carrying capacity, etc., and thus a logistic model should be used over an exponential one. Major paper in the density-dependent wars (see McPeck 2008). See Hey 1992 for an early introduction of this sort of model (Moran process).

Rabosky, D. L. 2009. Extinction rates should not be estimated from molecular phylogenies. *Evolution* 64:1816-1824.

"Here, I explore the consequences of violating a common assumption made by studies of extinction from phylogenetic data. I show that when diversification rates vary among lineages, simple estimators based on the birth-death process are unable to recover true extinction rates. This is problematic for phylogenetic trees with complete taxon sampling as well as for the simpler case of clades with known age and species richness. Given the ubiquity of variation in diversification rates among lineages and clades, these results suggest that extinction rates should not be estimated in the absence of fossil data."

Wertheim, J. O. and M. J. Sanderson. 2010. Estimating diversification rates: How useful are divergence times? *Evolution* 65:309-320.

Deals more with divergence time dating than with diversification analyses, per se: "We focus on two basic questions and one simple diversification model. In a pure-speciation Yule process, how well can the speciation rate be estimated when divergence times have error? And, how well behaved are statistical tests that compare the diversification of two sister clades? In general, we find that rate

estimation is often limited more by the size of the clade than the amount of sequence data used to infer ages, and hypothesis testing on rates is quite insensitive to inaccurate dates." Although, it has some very interesting stuff on the distributions underlying diversification analyses, including: "Before describing estimators and tests for these cases, we mention an important technical problem: the formalization of the statistical universe for assessing confidence for diversification problems ... One approach is to regard an instance of a diversification process that unfolds in time T producing N taxa as one of many that have the same age, T (Kendall 1949) but different numbers of taxa, N (N is thus a random variable). Another is to regard it as one of many that produced the same number of taxa, N , but a diversity of ages (Moran 1951; T is thus the random variable)" (311).

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