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TESTING THE STOCHASTICITY OF PATTERNS OF ORGANISMAL DIVERSITY: AN IMPROVED NULL MODEL

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Evolutionary biologists, systematists, and paleontologists studying patterns of diversity represented by different taxa, both extinct and extant, have tended to develop deterministic explanations for certain distinctive patterns. For example, Peterson (1983) hypothesized that the evolution of a subdigital pad in anoline lizards, unknown elsewhere in the family Iguanidae, is probably a strong explanation for why anoline lizards are so diverse (currently at approximately 250 species). The literature is replete with hypotheses of this kind.

In a series of papers, a group of paleontologists (the "Woods Hole group") criticized the practice within their field of failing to consider null models in studies of diversity. They suggested that patterns of diversity might be due to chance alone and thus not require specific explanations (Raup et al. 1973; Raup and Gould 1974; Schopf et al. 1975; Gould et al. 1977; Raup 1977). For example, Raup and Marshall asked "Did the order Creodonta die out because of the 'creodontness' of its genera (meaning small cranial volume and presumably low intelligence), or did the order die out just because all its genera went extinct through independent and widely varying causes?" (1980, p. 10). These and other approaches (Van Valen 1973; Anderson and Anderson 1975; Raup and Marshall 1980; Stanley et al. 1981; Savage 1983; Gilinsky and Bambach 1984, 1986) to the problem of stochasticity in the evolution of diversity can be divided between qualitative and quantitative methods. Qualitative methods have compared the results of computer simulations (e.g., Raup et al. 1973) or Monte Carlo models (e.g., Anderson and Anderson 1975) to real patterns of diversity without quantifying the probability of the outcomes. Quantitative approaches have tested real patterns of diversity against statistical null hypotheses. Generally, the quantitative approaches (e.g., Raup and Marshall 1980; Stanley et al. 1981) have tested the likelihood of fluctuations in absolute numbers of taxa within more-inclusive taxa under a null model incorporating a statistically estimated parameter of average change for the group in question. These methods are hereafter referred to as *absolute* methods. We argue that quantitative *relative* methods, defined as methods that test the likelihood of the size of one group relative to a related group, are more appropriate.

Raup et al. (1973), using a ground-breaking approach, developed a computer

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simulation (the MBL program) to randomly produce artificial histories characterized by integer-valued changes in the standing diversity (defined as the number of species extant at any given time) of "monophyletic groups" under the constraint of an equilibrium diversity. They found that the stochastic histories tended to resemble observed ones; their simulation produced diversity "explosions" as well as the complete extinction of taxa, patterns typically observed in the fossil record. Thus, they concluded that stochastic factors may play an important role in the genesis and extinction of diversity, and therefore, paleontologists should avoid idiographic explanations for the history of particular lineages. They argued that, instead, paleontologists should seek to create more-generalized, or "nomothetic," explanations for diversity histories. They suggested that each speciation and extinction had an antecedent cause but that the individual causes might be unrelated or unconnected, such that the observed pattern is the result of chance. In other words, individual determinism cannot be extrapolated to the level of the entire population (Schopf 1979). For example, consider a simple random walk generated by flipping a coin: each time a head occurs, a point on a Cartesian coordinate system is moved one unit upward on the y-axis; every time a tail is thrown, the point moves one unit down. The point often remains above or below the x-axis for many successive trials; yet we would never attempt to explain such behavior, which is the result of chance alone. Each head has a specific cause involving innumerable variables, but successive heads are not related or connected by their individual causes. This serves to illustrate another point, namely, that randomness does not imply disorder; surprisingly counterintuitive results can be generated from randomness (Raup 1977). Therefore, one has to exercise caution when creating deterministic explanations for apparent patterns.

The approach of Raup et al. (1973) is an important one. However, for the following reasons, improvements are necessary. First and foremost, their method did not determine quantitatively whether real patterns of diversity could be distinguished from an expectation of randomness but, rather, noted that real patterns occasionally looked like computer-generated null models. Furthermore, the authors stated that the artificial groups generated by the MBL program are strictly monophyletic; yet, in reality, many are paraphyletic (in the sense of Hennig 1966). The use of non-monophyletic groups in analyses of the history of diversity introduces an element of arbitrariness (Patterson and Smith 1987). Lastly, the MBL program generates taxa between predetermined upper and lower bounds of size; such a routine introduces another element of arbitrariness.

Savage (1983) compared large numbers of four-, five-, six-, and seven-taxon trees taken from the literature with three models elucidated by Simberloff et al. (1981) predicting the expected proportions of the topological types possible given n taxa. He found that a randomly branching Markovian model best fit the empirical trees, thereby strengthening earlier arguments that speciation and extinction are largely stochastic with respect to which lineage will be next to diverge or disappear. A randomly branching Markovian model is a simple stochastic process whereby every branch in a growing tree has an equal probability of splitting (Bailey 1964). However, as we argue later, these results may apply to only small sets of closely related taxa.

Recent papers (Raup and Marshall 1980; Stanley et al. 1981; Gilinsky and Bambach 1984, 1986) have challenged the view that much of the history of diversity is stochastic. Using what they considered to be refined methods for studying diversity, they concluded that real diversity histories were not stochastic but displayed significant nonrandom order. Stanley et al. (1981), using an absolute method, argued that the MBL program of Raup et al. (1973) suffered from not using empirically scaled parameters (probabilities of branching, persistence, and extinction, and appropriate levels of standing diversity at time zero). They developed a computer simulation and an analytic method for testing whether changes in the standing diversity of post-Cambrian Paleozoic orders of brachiopods could have occurred by chance. Their findings strongly supported the alternative hypothesis that clade expansions and contractions in post-Cambrian Paleozoic brachiopods did not occur by chance but had definite causes. We believe, however, that their approach was flawed for several reasons. By testing changes in absolute numbers of taxa through time, two potentially deterministic phenomena were confused: the evolution of differences in the probabilities of speciation and/or extinction among lineages, and nonrandom changes in numbers of taxa through time over many lineages. The former may result from the evolution within species of biological innovations ("key adaptations"), whereas the latter results from large-scale, extrinsic changes affecting many lineages simultaneously. For example, environmentally induced mass extinction is an example of a large-scale change affecting many lineages simultaneously. The two kinds of determinism are distinct and should be tested separately. We believe that large-scale determinism is best tested using an absolute quantitative method, whereas determinism resulting in relative differences in the probabilities of speciation and/or extinction among lineages is best tested by the method we describe herein. The method of Stanley et al. (1981) fails to distinguish between the two types of change and, therefore, fails to test them separately. Furthermore, their method relies on the accuracy of the input-generating parameters, which are calculated as average rates. Using average rates, however, ignores the individual variation of taxa. Lastly, their method was applied to post-Cambrian orders of brachiopods; we wonder to what extent fluctuations in these orders are the result of differential sampling in the geologic record, differential preservation of brachiopods, or the inherent arbitrariness of taxonomy. These criticisms apply in general to absolute approaches to the problem of the stochasticity of evolution. In this paper, we focus only on the possible existence of intrinsic differences among lineages in probabilities of speciation and/or extinction (such as might occur as a result of an adaptation).

Raup and Marshall (1980), in another absolute method, tested whether generic turnovers, defined as rates of genera origination and extinction in orders of mammals, varied significantly from one another, thereby demonstrating deterministic differences in rates of speciation and extinction. Using a modified χ^2 test, they concluded that significant differences in generic turnover are a reality and coined the term "taxotely" for rates of turnover within lineages differing significantly from the rate of turnover among lineages. However, their findings could also have resulted from the same artifacts discussed in the preceding paragraph, those of the pitfalls of using taxonomy and the sampling of the fossil record (see criticisms in Cracraft 1981).

To date, we feel that the debate about stochasticity versus determinism in the evolution of diversity has not been adequately resolved because a quantitative method based purely on the topology of phylogeny has not been employed. The basic premise of our paper is that analysis of macroevolutionary patterns must be based on knowledge of relationships (Cracraft 1982). Much speciation and extinction among closely related species is probably stochastic (relative to which taxon speciates or goes extinct), as suggested empirically by Savage (1983), but stochasticity of large-scale patterns remains to be demonstrated. Earlier quantitative attempts to test the stochasticity of the pattern of diversity (Raup and Marshall 1980; Stanley et al. 1981; Gilinsky and Bambach 1984, 1986) suffered from not considering phylogeny as a specific topology. Herein we synthesize the work of others with some of our own to create a quantitative null model based on topology to test the randomness of large-scale pattern. Unlike the model of Stanley et al. (1981), our null model reflects only relative changes in the probabilities of speciation and extinction among lineages. Furthermore, phylogenetic topologies are independent of the artifacts discussed in the previous paragraphs. Our null model is an analytic model based on the mathematics of a simple, Markovian dichotomous-branching process (Harding 1971). The application of such a model has appeared before in studies of both phylogeny (e.g., Raup et al. 1973; Savage 1983) and vicariance biogeography (Simberloff et al. 1981; Simberloff 1987).

Our null model hypothesizes that the processes generating patterns of diversity (extinction and speciation) occur randomly among taxa and, therefore, that very large or very small organismal radiations, as compared with related taxa, are the result of chance. Morphological or genetic change is ignored (except to the extent that species are delimited by morphological or genetic criteria) because our model deals exclusively with the branching process of evolution reflected in the topology of a phylogeny. Because of the problems that arise from testing phylogenies of entirely extinct taxa, our null model is applicable only to the relationships of contemporaneous species. When extinct lineages are used, relative differences in extinction can no longer be tested; instead, only differential speciation can be considered. However, if significant differences are found, they could be the result of certain lineages' having slightly more extinct taxa than others and, therefore, fewer chances through time for speciation. Testing phylogenies of modern organisms avoids the artifacts associated with data based on the fossil record.

Our treatment of this subject differs from that of earlier papers (Raup et al. 1973; Anderson 1974; Raup and Gould 1974; Anderson and Anderson 1975; Schopf et al. 1975; Gould et al. 1977; Raup and Marshall 1980; Stanley et al. 1981; Gilinsky and Bambach 1984, 1986) in the following ways: (1) our conceptualization of the evolution of diversity is a topology resulting from a branching process (phylogeny) rather than an integer-valued process of change in total diversity; (2) extinct taxa are not included in phylogenies to be tested, and our method is therefore independent of the problems inherent in sampling the fossil record; (3) species rather than supraspecific taxa are the units of analysis (see Stanley et al. 1981), thereby eliminating the subjectivity of higher taxonomy (as discussed above, earlier papers—e.g., Raup and Marshall 1980; Stanley et al. 1981—have suffered from using methods sensitive to the artifacts resulting from taxonomy); (4) no unnecessary assumptions, such as equilibrium in the number of coexisting species (Raup et al. 1973), are made; and (5) our model is independent of the temporal effects on probabilities of extinction and/or speciation.

PHYLOGENETIC TREES

Our approach is based on a probabilistic study of large phylogenetic trees. We make only the following assumptions with respect to phylogenies.

1. The phylogeny of a set of contemporaneous species can be represented by a rooted tree comprising branches and nodes. The latter are divided between interior and terminal nodes; interior nodes are branching points, whereas terminal nodes are species. Such a tree is purely dimensionless in that no inferences about time of divergence or relative morphological change are possible; only relationships of common ancestry are shown.
2. All branching points are dichotomous; that is, they give rise to only two descendant branches. This common assumption in phylogenetic studies is not always accurate; however, we believe that polychotomous speciation is rare.
3. All species occupy only terminal positions, as they would if they were contemporaneous. In other words, no modern species is considered an ancestor of another.
4. Hybridization between species is considered a rare form of speciation and, therefore, is ignored in our treatment.
5. Allochronic speciation, or the formation of new species simply through sufficient anagenetic evolution along a lineage, is ignored. New species form only by the splitting of lineages.

Trees of this nature—that is, trees in which the terminal nodes are labeled and the interior nodes are hypothetical, unlabeled points—are the type of trees most commonly used in modern phylogenetic studies of contemporaneous organisms. When the interior nodes are constrained to be dichotomous, the total number of distinguishable rooted trees possible, $D(n)$, is a function of n taxa:

$$D(n) = (2n - 3)!/2^{n-2}(n - 2)! \tag{1}$$

(Felsenstein 1978), where $n \geq 2$.

Consider five taxa; from equation (1) there are 105 ways in which five taxa can be interrelated. These trees sort into three topological types (fig. 1). The number of topological types is simply the number of distinct trees that would exist if the taxon labels were deleted. Another way to understand topological types is to consider the result of deleting interior nodes: if the basal node of tree B in figure 1 were deleted, it would result in two subtrees of two and three taxa. Thus, it differs from trees A and C, each of which has a basal node connected to subtrees of one and four taxa. Trees A and C can be distinguished from each other by the next interior node up from the basal node. Topological types are important to our treatment because probabilities can be associated with them (see below). The number of such topological types, $N(n)$, can be found using a recursive formula

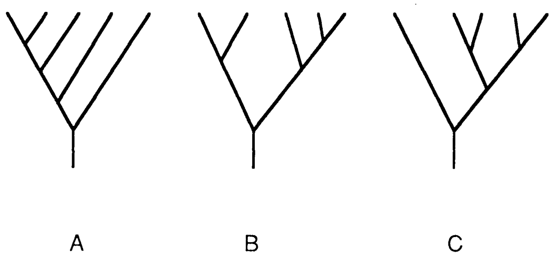

FIG. 1.—The three distinct topological types on five taxa.

given by Wedderburn (1922):

$$N(n) = \left[\frac{1}{2}\sum_{k=1}^{n-1} N(k)N(n-k)\right] + E(n)\ , \tag{2}$$

where

$$E(n) = \begin{cases} \tfrac{1}{2}\, N(n/2) & \text{if } n \text{ is even} \\ 0 & \text{if } n \text{ is odd} \end{cases}$$

and where $N(1) = 1$.

The number of ways in which n taxa can be interrelated, $L(T)$, within a topological type T is given by a pair of recursive expressions (Harding 1971, p. 72). If deletion of the basal node (root) partitions the topological type, T, into two subtrees R and S, of size r and s, respectively, such that $r \leq s$, then

$$L(T) = \binom{n}{r} L(R)L(S) \qquad \text{if } R \neq S \tag{3}$$

or

$$L(T) = \tfrac{1}{2}\binom{n}{r} L(R)^2 \qquad \text{if } R = S\ , \tag{4}$$

where $L(T) = 1$ for $n = 1$.

PROBABILITIES OF TREES

Simberloff et al. (1981), in considering the probability under the null model of replicating trees as applied to the testing of vicariance biogeography, discussed several alternatives: (1) each topological type is equiprobable; (2) every distinguishable tree, as given in equation (1), is equiprobable; or (3) each topological type occurs in the proportions predicted by a randomly branching Markovian model. The implicit assumption in many previous works (e.g., Rosen 1978) has been that every individual tree is equally probable. If true, then trees A, B, and C of figure 1 would occur randomly in the proportions 60/105, 30/105, and 15/105, respectively (the numerators are simply the number of trees for that topological type as given by eqs. 3, 4). But as Simberloff et al. (1981) argued, no logical justification exists for this assumption; why, they asked, should the topological

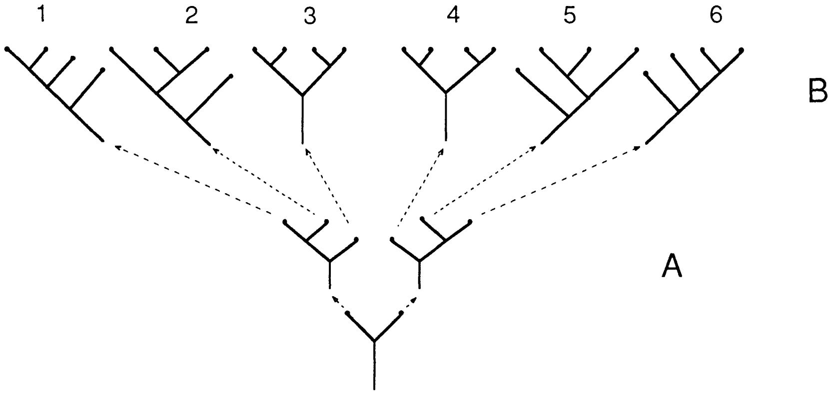

FIG. 2.—A diagrammatic representation of the process of lineage-splitting leading to four taxa.

type of tree A in figure 1, for example, occur in direct proportion to the number of distinct combinations among its terminal species? This hidden assumption is derived from the assumption that all trees, the number of which is given by equation (1), are equiprobable. They argued that one of the two alternatives listed above (2 or 3) is more plausible. The former seems entirely arbitrary; Savage (1983), using trees taken from the literature, found that the topological-types-are-equiprobable hypothesis is a poor predictor of observed tree proportions, but that the Markovian model is a good predictor of observed tree proportions.

Under the Markovian model, the probability of speciation is equally distributed along all branches in a growing phylogeny. To generate all possible outcomes in a Markovian framework, we need a different perspective on phylogeny than the one offered by equation (1), which gives the number of ways in which n named taxa can be interrelated. Instead, we need to view the process of phylogeny from the perspective of an ancestral species splitting to give rise to distinct descendant species. Figure 2 is a diagrammatic representation of the process by which lineage splitting leads from one ancestral species to four. As shown, there are six possible ways to generate four species from such a process: initially, an ancestral species splits to give two distinct species; depending on which of the two species splits, two possibilities exist (fig. 2, step A); depending on which of the three species splits in each of the diagrams in step A, six possibilities result (fig. 2, step B). Harding (1971, p. 63) has shown that the number of such trees possible, $P(n)$, from a simple lineage-splitting process is

$$P(n) = (n - 1)!. \tag{5}$$

Table 1 gives $P(n)$, $D(n)$, and $N(n)$ for up to 15 taxa. Given an equal probability of speciation along every branch in a growing phylogeny, every tree in figure 2 is equiprobable. The topological type represented by trees 1, 2, 5, and 6 occurs four times, whereas the topological type represented by trees 3 and 4 occurs twice; therefore, the probabilities of these types are $4/6$ and $2/6$, respectively. Harding (1971, p. 64) gave a pair of recursive equations for calculating the Markovian

TABLE 1

THE NUMBER OF POSSIBLE TREES OF THREE TYPES FOR UP TO FIFTEEN TAXA

n	$P(n)$	$N(n)$	$D(n)$
1	1	1	1
2	1	1	1
3	2	1	3
4	6	2	5
5	24	3	105
6	120	6	945
7	720	11	10,395
8	5,040	23	135,135
9	40,320	46	2,027,025
10	362,880	98	34,459,425
11	3,628,800	207	654,729,075
12	39,916,800	451	13,749,310,575
13	479,001,600	983	316,234,143,225
14	6,227,020,800	2,145	7,905,853,580,625
15	87,178,291,200	4,816	213,458,046,676,875

NOTE.—$P(n)$ is the number of phylogenies resulting from a simple lineage-splitting process leading to n species and is given by equation (5) in the text. $N(n)$, the number of topological types of the phylogenies $P(n)$ and $D(n)$, is given by equation (3). $D(n)$, the number of ways that n taxa can be interrelated, is given by equation (1).

probability $p(T)$ for each topological type T on n taxa:

$$p(T) = 2(n - 1)^{-1}p(R)p(S) \qquad \text{if } R \neq S \tag{6}$$

or

$$p(T) = (n - 1)^{-1}p(R)^2 \qquad \text{if } R = S, \tag{7}$$

where $n \geq 2$ and $p(T) = 1$ for $n = 2$ or 3. Table 2 gives the Markovian probabilities for up to eight taxa.

To find the probability of an individual tree with labeled taxa, one divides the probability of its topological type by the number of such trees within that type (as found by eqs. 3, 4). For example, the Markovian probability of the topological type represented by tree B in figure 1 is ½; the probability of any tree within this type, say (((A,B)C)(D,E)), where parentheses surround monophyletic groups, would be $0.5/30 = 0.017$. It is interesting to note that a tree of type B in figure 1 is more than twice as probable as a tree of type A; this asymmetry of probabilities is an inherent characteristic of the Markovian model of tree probabilities. Harding (1971, p. 73) gave a recursive equation relating the probability of a specific labeled tree, T_1, within T:

$$p(T_1) = 2[r!(n - r)!]p(R_1)p(S_1)/(n - 1)n! \tag{8}$$

for both $R \neq S$ and $R = S$, where $p(T_1) = 1$ for $n = 1$.

We feel that a Markovian process of random branching is the proper null model for testing the stochasticity of phylogenies. But to make any consideration of the evolution of diversity realistic, one must consider extinction. Many extant taxa probably have experienced the extinction of some of their subtaxa in the past;

TABLE 2

THE RANDOM PROBABILITIES OF ALL TOPOLOGICAL TYPES FOR UP TO EIGHT TAXA

Type	Probability	Type	Probability	Type	Probability
1	1	$7_3 = 1 + 6_3$	1/15	$8_8 = 1 + 7_8$	1/63
2	1	$7_4 = 1 + 6_4$	4/45	$8_9 = 1 + 7_9$	1/21
$3 = 1 + 2$	1	$7_5 = 1 + 6_5$	2/45	$8_{10} = 1 + 7_{10}$	4/63
$4_1 = 1 + 3$	2/3	$7_6 = 1 + 6_6$	1/15	$8_{11} = 1 + 7_{11}$	2/63
$4_2 = 2 + 2$	1/3	$7_7 = 2 + 5_1$	1/9	$8_{12} = 2 + 6_1$	4/105
$5_1 = 1 + 4_1$	1/3	$7_8 = 2 + 5_2$	1/18	$8_{13} = 2 + 6_2$	2/105
$5_2 = 1 + 4_2$	1/6	$7_9 = 2 + 5_3$	1/6	$8_{14} = 2 + 6_3$	2/35
$5_3 = 2 + 3$	1/2	$7_{10} = 3 + 4_1$	2/9	$8_{15} = 2 + 6_4$	8/105
$6_1 = 1 + 5_1$	2/15	$7_{11} = 3 + 4_2$	1/9	$8_{16} = 2 + 6_5$	4/105
$6_2 = 1 + 5_2$	1/15	$8_1 = 1 + 7_1$	4/315	$8_{17} = 2 + 6_6$	2/35
$6_3 = 1 + 5_3$	1/5	$8_2 = 1 + 7_2$	2/315	$8_{18} = 3 + 5_1$	2/21
$6_4 = 2 + 4_1$	4/15	$8_3 = 1 + 7_3$	2/105	$8_{19} = 2 + 5_2$	1/21
$6_5 = 2 + 4_2$	2/15	$8_4 = 1 + 7_4$	8/315	$8_{20} = 3 + 5_3$	1/7
$6_6 = 3 + 3$	1/5	$8_5 = 1 + 7_5$	4/315	$8_{21} = 4_1 + 4_1$	4/63
$7_1 = 1 + 6_1$	2/45	$8_6 = 1 + 7_6$	2/105	$8_{22} = 4_1 + 4_2$	4/63
$7_2 = 1 + 6_2$	1/45	$8_7 = 1 + 7_7$	2/63	$8_{23} = 4_2 + 4_2$	1/63

NOTE.—Data from Harding 1971, p. 66. Notation for topological types is based on a recursive system with subscripts denoting the specific type.

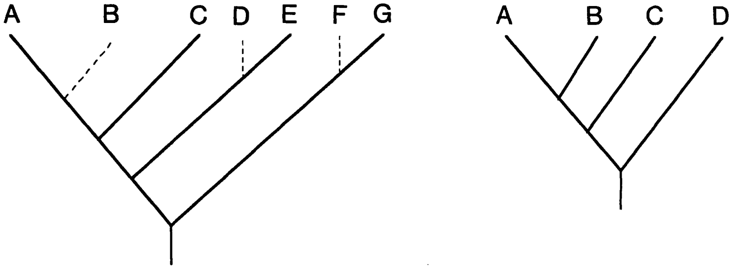

FIG. 3.—A phylogeny with extinct lineages depicted as dashed lines (*left*), and the phylogeny as it would appear if only extant taxa were considered (*right*).

such taxa, in a study of modern organisms, are "invisible" (see fig. 3). It can easily be shown analytically that the Markovian equations presented above still apply when extinction is incorporated, as long as the probability of extinction is equal among all branches in a growing phylogeny. Therefore, our null model tests whether probabilities of speciation and/or extinction differ significantly among lineages. The two factors are inextricable; determining which of the two causes was responsible for particular patterns is impossible.

TESTING THE NULL MODEL: THE METHOD

Because Savage (1983) showed that small (four-, five-, six-, and seven-taxon) empirical trees follow a simple stochastic Markovian distribution, we assumed earlier that the processes of speciation and extinction among closely related taxa are essentially stochastic. This seems reasonable, since one might expect closely related species to be biologically similar. Therefore, one species is probably no more prone to speciation or extinction than a closely related species. Thus, a Markovian model is the appropriate null model to apply to studies such as vicariance biogeography (see Simberloff 1987) that generally compare small phylogenies. However, we do not think that stochasticity necessarily can be extrapolated to larger patterns, that is, larger phylogenies ($n \gg 7$). Given enough time, a branch in a growing phylogeny might evolve differences in biology that predispose that branch and its descendants to increased and/or decreased rates of speciation and/or extinction. If the evolution of such features occurs infrequently, then random sampling of small portions of the overall phylogeny of life would reveal a stochastic pattern; in most cases, the sampled phylogenies would be too small to reflect the infrequent occurrences of these features. Thus, the large-scale nonrandom pattern that might be the reality of phylogeny would be masked. The evolution of innovations (adaptations) predisposing certain lineages to increased and/or decreased rates of speciation and/or extinction, if they occur, would be analogous to synapomorphies (in the sense of Hennig 1966) and can be mapped on phylogenetic trees.

Testing whether or not such shifts in the probabilities of speciation and extinction really occur requires sampling large phylogenies ($n \gg 7$) and testing them quantitatively for their fit to the Markovian null model. By sampling large phylogenies, especially ones postulated to represent nonrandom pattern, the probability is increased of including one with an evolutionary shift in rates of speciation and/or extinction. However, by sampling clades hypothesized to represent nonrandom patterns, one biases toward rejection of the null model; even a stochastic model predicts apparently nonrandom outcomes (i.e., one should not test the randomness of phylogeny by choosing apparently nonrandom phylogenies). This can be obviated by testing the distribution of several to many large phylogenies chosen randomly, rather than just one phylogeny, against the null model. A rejection of the null model establishes only that deterministic diversity evolution occurs, not whether individual phylogenies require deterministic explanations; we will probably never know whether the radiation of anoline lizards represents nonrandom evolution. In this sense, our null model is nomothetic; it can only establish whether the evolution of diversity behaves randomly in a statistical sense.

To test the distribution of phylogenies, we first need a means of assessing the probabilities of individual phylogenies in a relative framework, since our null model seeks to test whether clades are too large or too small, as expected by chance, compared to related taxa. This can be done by extending our equations on the probabilities of trees to include sister groups. A *sister group* is the group of organisms most closely related to a specified taxonomic group; they are the rooted subtrees that remain when an interior node is deleted (fig. 4). Any member of a sister group is more closely related to any member of the other sister group than to any taxon lying outside the clade defined by the two sister groups. Sister groups are especially well suited to our analysis because, by definition, sister groups are of equal age (Cracraft 1981) and therefore represent historical equivalents. Thus, sister groups are the appropriate units for comparison in testing whether rates of speciation and/or extinction vary significantly between lineages (Cracraft 1981).

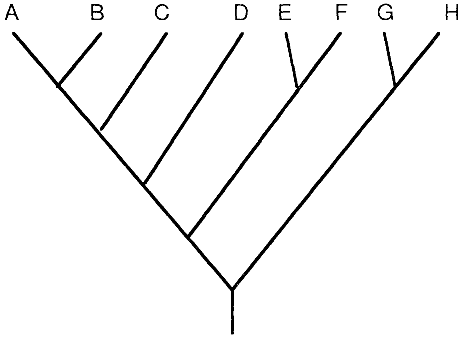

FIG. 4.—A representation of a phylogeny for which the taxa A, B, C, D, E, and F are the sister group to taxa G and H.

Consider the tree of figure 4. The probability that an ancestral species would split into two sister species, of which each would subsequently give rise to six species and two species, respectively, would simply be the sum of the Markovian probabilities of all topological types possible given the partition of the tree into two subtrees of size six and two, represented as 2,6 (herein, the notation r,s is used to denote the situation in which the root of a tree or subtree gives rise to two descendant subtrees of size r and s, respectively; it does not indicate an ordered pair). The number $S(r,s)$ of all topological types given a partition r,s is

$$S(r,s) = N(r)N(s) \qquad \text{if } r \neq s \tag{9}$$

or

$$S(r,s) = N(r) + \binom{N(r)}{2} \qquad \text{if } r = s\,, \tag{10}$$

where $N(r)$ and $N(s)$ are given by equation (2).

The partition of the tree in figure 4, 2,6, corresponds to six distinct topological types. The probability of this partition would then be the sum of the probabilities of each of these individual topological types. The probability $p(r,s)$ of any partition r, s can be represented as

$$p(r,s) = \sum_{i=1}^{S(r,s)} p(T_i)\,, \tag{11}$$

where T_i denotes the ith topological type. The quantity $p(r,s)$ can be found by calculating the probabilities of each individual topological type from equations (6) and (7) and summing them. Obviously, this becomes tedious for large numbers of species. The right-hand terms of equations (6) and (7), however, sum to unity over all $S(r,s)$, thereby transforming equations (6) and (7) from recursive formulas to simple equations (see the Appendix for proof):

$$p(r,s) = 2(n - 1)^{-1} \qquad \text{if } r \neq s \tag{12}$$

or

$$p(r,s) = (n - 1)^{-1} \qquad \text{if } r = s\,. \tag{13}$$

This simplifies calculations of the Markovian probabilities for very large sister-taxa comparisons. From equations (12) and (13), the probability of the partition represented by the tree in figure 4 is $2/7$. One important characteristic of these equations is that for any number of taxa, n, the distribution of probabilities for all $\lfloor n/2 \rfloor$ values of r,s (where $\lfloor x \rfloor$ is a function that assigns to every value of x the greatest integer not greater than x) is nonmodal: $p(r = 1, s = n - 1) = p(2, n - 2) = \ldots = p(\lfloor n/2 \rfloor, \lfloor n/2 \rfloor + 1$ if n is odd, or $2p(n/2, n/2)$ if n is even). This surprising characteristic of the Markovian model predicts that unbalanced sister taxa will occur fairly frequently. That is, a Markovian randomly branching process inherently produces apparently nonrandom patterns. This results because there are more possible component topological types for unbalanced partitions. For example, the partition 1,14 corresponds to 2145 possible types, whereas the more-balanced 7,8 corresponds to just 253 possible topological types. The fact that sister taxa of disparate sizes are, in fact, relatively probable underscores the need for statistical testing of the kind described in this paper; it is untenable to assume that any pair of sister taxa differing in size require some sort of specific hypothesis to explain that disparity.

The cumulative probability of a partition $p_c(r,s)$ can be calculated by summing the probabilities of all partitions more extreme plus $p(r,s)$. For 6,2, $p_c(r,s)$ is $p(6,2) + p(7,1) = 4/7$. This has the effect of "locating" the partition within the distribution of partitions. Equations (12) and (13) can be modified to give $p_c(r,s)$:

$$p_c(r,s) = 2r(n-1)^{-1} \qquad \text{for } r \neq s \text{ and where } r < s \tag{14}$$

or

$$p_c(r,s) = 1.0 \qquad \text{for } r = s\,. \tag{15}$$

A specific example to illustrate the use of equations (14) and (15) is the large radiation of anoline lizards of the family Iguanidae distributed throughout subtropical and tropical regions of the Caribbean Basin, Central America, and North and South America. Anoles, with approximately 250 species, are commonly thought to represent an example of nonrandom evolution requiring some kind of deterministic explanation. Anoles are most closely related to the Cuban genus *Chamaeleolis* (Guyer and Savage 1986), comprising only three species (Schwartz and Henderson 1985). The cumulative probability of an ancestral species splitting to eventually yield sister groups of 3 and 250 species is $p(3,250) + p(2,251) + p(1,252) = 0.024$.

To test the distribution of large phylogenies, many should be chosen in an unbiased fashion (i.e., without respect to disparity in size of sister groups) and compared with the predictions of the null model. The distribution of values for $p_c(r,s)$ (generated by eqs. 14, 15) over different numbers of taxa, n, is continuous and nonmodal. If we arbitrarily delimit probability classes from 1.0 to 0, say 1.0 to 0.9, 0.9 to 0.8, . . . , 0.1 to 0, then the theoretical distribution of cumulative probability values (over different numbers of taxa) falling within these classes will be nonmodal when a large number of phylogenies is sampled; that is, each class will contain approximately equal numbers of entries. Hence, it is a straightforward matter to statistically test the null hypothesis by a χ^2 or some other goodness-of-fit test. If C classes are delimited, into which are distributed the empirical observations, then the expected number of observations per class will be K/C, where K is the overall number of phylogenies sampled. If the above procedure leads to rejection of the null model, it suggests that too many sister-taxa observations are falling into certain classes and thus that the evolution of diversity cannot be characterized as purely random. This kind of testing is a prerequisite before deterministic explanations can be created for taxonomic patterns. If determinism is ultimately found to be a reality, it could result from intrinsic and/or extrinsic causes. Intrinsic causes would include adaptations that predispose taxa to increased rates of speciation or decreased rates of extinction. Extrinsic causes might include phenomena such as a taxon's developing an increased rate of speciation because of tectonic activity over its range.

SUMMARY

Evolutionary biologists, systematists, and paleontologists commonly have invoked deterministic explanations for certain patterns of diversity. However, few authors have considered the null model that the factors generating diversity may behave stochastically and that "pattern" therefore results from chance and does not require a deterministic explanation. We have developed a quantitative null model based on a randomly branching Markovian process to test the stochasticity of patterns of diversity as represented by phylogenies of contemporary organisms. The model allows one to consider real phylogenies containing large numbers of taxa and to determine whether the observed topology of those phylogenies might be explained by chance alone. We believe that our null model represents an improvement over earlier models. The simplicity of our null model makes feasible the testing of large numbers of phylogenies for stochasticity.

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APPENDIX

The following is a proof for the transition of equations (6) and (7) to equations (12) and (13).

For r ≠ s.—The problem of calculating $p(r,s)$ for $r \neq s$ is one of finding the probability of a topological type given r taxa, multiplying it by the probability of any topological type given s taxa, and multiplying the result by $2\,(n - 1)^{-1}$. This is done for all topological types on s taxa and then repeated for all topological types on r taxa; the results are summed to give $p(r,s)$. The individual probabilities for all topological types given r taxa can be denoted as $X_1, X_2, \ldots, X_{N(r)}$, and the individual probabilities for all topological types given s taxa can be denoted as $X_{N(r)+1}, X_{N(r)+2}, \ldots, X_{N(r)+N(s)}$. Using equation (6),

$$\begin{aligned} p(r,s) &= 2(n-1)^{-1}X_1X_{N(r)+1} + 2(n-1)^{-1}X_1X_{N(r)+2} + \ldots \\ &\quad + 2(n-1)^{-1}X_2X_{N(r)+1} + 2(n-1)^{-1}X_2X_{N(r)+2} + \ldots \\ &\quad + 2(n-1)^{-1}X_{N(r)}X_{N(r)+N(s)} \\ &= 2(n-1)^{-1}\sum_{i=1}^{N(r)}\ \sum_{j=N(r)+1}^{N(r)+N(s)} X_iX_j\,. \end{aligned}$$

Given that the two sets of probabilities always sum separately to 1.0, the double sum in the above equation will always sum to 1.0. Thus, $p(r,s) = 2(n-1)^{-1}$ for $r \neq s$.

For r = s.—In this situation, the two sets of topological types on r and s taxa and their probabilities are identical. Hence, some topologies given r,s will be symmetrical ($R = S$), whereas others will be asymmetrical ($R \neq S$), necessitating calculation of $p(r,s)$ using both equations (6) and (7). There will be exactly $c[N(r),2]$ (the binomial coefficient) topologies where $R \neq S$ and $N(r)$ topologies where $R = S$. Using equations (6) and (7),

$$\begin{aligned} p(r,s) &= 2(n-1)^{-1}\sum_{i\neq j} X_iX_j + (n-1)^{-1}\sum_{i=1}^{N(r)} X_i^2 \\ &= (n-1)^{-1}\left(2\sum_{i\neq j} X_iX_j + \sum_{i=1}^{N(r)} X_i^2\right). \end{aligned}$$

Given that the right-hand term will always equal 1.0 as long as the sequence X_i sums to 1.0, $p(r,s) = (n-1)^{-1}$ for $r = s$.

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