supports?" Because uniform topological priors imply inappropriately informative clade priors, the latter interpretation is required. The Bayes factor (Jeffreys, 1960) allows an interpretation of such posteriors; it estimates how the evidence at hand has borne out prior assertions, regardless of how meaningful these priors are. Pickett and Randle (2005) advocated the use of Bayes factors when non-uniform clade priors are used, for this exact reason. If we do not interpret clade posteriors as a measure of evidentiary support, but they are also not reflections of actual prior knowledge or ignorance, one must ask what is the benefit of invoking a prior distribution at all.

Brandley et al. claim that the undesirable influence of priors, regardless of their design, is unimportant, because the prior is eventually overwhelmed. Brandley et al. suggest that advocates "hope" that "inappropriately informative" priors will either be overwhelmed or, if possible, avoided altogether. And so, it seems, they want their phylogenetic hypothesis to be free of prior influence, one way or another. Why make prior assertions if the goal is to eliminate their influence? If this goal is desired, then "we may solve the real problem directly" (Fisher, 1912:156), by employing a method that avoids the confounding effects of priors from the start; that method is maximum likelihood.

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Time, Species, and the Generation of Trait Variance in Clades

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No consensus has developed concerning the mechanism of phenotypic diversification among species within clades. Eldredge and Gould (1972) and Gould and Eldredge (1977) proposed an alternative to the then prevailing view among evolutionary biologists that evolution occurred by frequent small steps along branches of a phylogeny (anagenesis). Instead of this phyletic, or gradual evolution, they pointed to evidence from the paleontological record suggesting occasional dramatic episodes of morphological change separated by periods of stasis. They associated shifts in their "punctuated equilibrium" model with speciation events (cladogenesis), and invoked a mechanism of "genetic revolution" linked to species formation in small, isolated peripheral populations (Mayr, 1963) to produce sudden change unrelated to selective pressures in the environment. Similar mechanisms referred to as "founder flush" and "transilience" also require population

bottlenecks (see Barton and Charlesworth, 1984; Carson and Templeton, 1984). Although genetic revolution and related models of species formation have little following at present (Coyne and Orr, 2004), one cannot discount the possibility of rapid phenotypic change associated with the production of species. Ecologists interested in phenotypic diversification, beginning with Lack (1947, 1971), Grant (1972, 1986), and others, and continuing through more recent discussions of adaptive radiation (Givnish and Sytsma, 1997; Schluter, 2000), have emphasized the role of diversifying selection applied by species interactions within clades to explain the evolution of phenotypic differences between species.

Despite intense interest in diversification during the past 30 years, including substantial work by paleontologists (Raup and Gould, 1974; Foote, 1997; Wagner, 1997; Ciampaglio et al., 2001), few clade-wide tests of mechanisms have been attempted (Mooers et al., 1999; Pagel, 1999). Experimental studies have revealed the power of competition and predation as agents of selection on morphology in natural systems (e.g., Reznick, 1982; Reznick and Bryga, 1987; Reznick et al., 1990; Schluter, 1994, 1996). However, the insights gained in these studies cannot be extrapolated to entire clades over the long history of their evolution unless one assumes that mechanisms are invariant over a broad range of scales. The recent availability of phylogenetic hypotheses for large clades has motivated analytical approaches to understanding temporal patterns in species diversification (Nee et al., 1992; Harvey et al., 1994; Mooers et al., 1999; Harvey and Rambaut, 2000; Heard and Mooers, 2002), and, when applied to phenotypic traits, temporal patterns of morphological change (Mooers et al., 1999; Pagel, 1999; Bokma, 2002). These analyses hold some promise of revealing mechanisms of phenotypic change, particularly because rates of morphological and molecular evolution are typically uncoupled (Bromham et al., 2002). However, extinct taxa, restricted taxon sampling, an apparent correlation between molecular phylogenetic branch-lengths and net speciation rate (Webster et al., 2003), and broad confidence limits on parameter estimates remain significant problems.

Recently, I described an approach for partitioning the contributions of time-dependent and speciation-dependent mechanisms to the variance in phenotypic traits within a clade (Ricklefs, 2004a). The method rests on the premise that although variance accumulates linearly with time under both mechanisms, the contributions of the two can be separated when the ages of clades and the numbers of speciation events are at least partly independent. I used multiple regression to assess the statistical effects of clade age and the log-transformed number of species on morphological variance in clades of passerine birds (Aves: Passeriformes). This statistical technique partitions the variance in morphology into amounts uniquely related to each of the independent variables and amounts associated with the correlation between the two independent variables. In my analyses, time (clade age) had no unique statistical influence on morphological variance whereas the logarithm of species number did, and I concluded that diversification was either associated with speciation events or responsive to species interactions within clades.

Purvis (2004) criticized this approach, claiming from the results of simulations of random morphological evolution over randomly diversifying clades that one could not distinguish the effects of species number and time on morphological variance. Although I believed that Purvis's analysis was not definitive (Ricklefs, 2004b), I was also struck by a misconception concerning the generation of variance. Purvis stated, "Under gradual change, variance accumulates along phylogenetic branches. Larger clades have more total branch length within them, even in same-aged clades, and so have more variance in gradually evolved traits." Taken at face value, this statement is incorrect. Moreover, this error regarding a fundamentally important point apparently is widely held among evolutionary biologists: the four reviewers of Purvis's comment together with my response largely agreed with Purvis's assessment. Here, I clarify how phenotypic variance is generated in randomly evolving clades. I also simulate diversification within phylogenetic trees structured to reveal the different effects of species proliferation and time-dependent change on phenotypic variance, using a purely empirical approach. The results of this exercise show that Purvis was correct in saying time-dependent and speciation-dependent variance generation cannot be distinguished by the approach that I proposed. However, it is also clear that variance depends on the average separation in time between species, and not on total branch length.

The Accumulation of Variance

Assume that speciation and extinction are homogeneous stochastic processes with constant rates. Phenotypic traits change by a random increment at each iteration step (time-dependent) or speciation event (speciation-dependent). The increment in a trait value (x) can be either continuous (e.g., drawn from a normal distribution with mean = 0 and standard deviation = 1) or discrete (e.g., +1 or −1). The value of x has no upper or lower bound. This is equivalent to the Brownian motion model of Felsenstein (1985); the simulations discussed here pertain only to such random walks, although phenotypic space in natural systems almost certainly is bounded (Foote, 1995; Wagner, 2000).

When the phenotypes of several independently evolving lineages change according to the same time-dependent random process, the variance in phenotypic value among them increases as a linear function of time. This has been shown analytically, for example by Slatkin (1981) and Gavrilets (1999), and through simulation by Valentine et al. (1994). Because time-dependent (anagenic) variances accrued during each successive increment (v_a) add to produce the variance in the trait values at some time t, the trait values of the independent evolutionary branches form a distribution with expected variance $V = v_a t$. This is also the expected

variance between any two branches picked at random. Thus, the variance among all the branches is identical to the average variance between pairs of branches. That is, the expected variance between two observations drawn from a distribution is the same as the expected variance among a larger number of observations drawn from the same distribution. Variance is independent of the sample size; hence, it is independent of total branch length within a clade.

Consider a speciation-dependent (cladogenic) process in which the trait value x changes by an increment having a variance of v_c at each speciation event. If the speciation rate were s events per unit time, the expected accumulation of variance among independent single lineages would be equal to v_c times the number of branch points in the history of those lineages (st). When daughter lineages both change at their initial branch point, two sister lineages start with variance v_c at time 0 and the accumulated variance since their splitting is $V = v_c st + v_c$, or $v_c(st + 1)$. The total variance generated depends on the rate of speciation, i.e., the number of speciation events per lineage, and not the number of species in the clade. However, because variation in s determines both the variance accumulation and the number of lineages (N), even though the generation of variance is time-dependent, the variance generated is related both to time and to the logarithm of the number of species, as Purvis (2004) has said.

Can one use the variance in a phenotypic trait to separate the contributions of time-specific and speciation-specific mechanisms of evolutionary change? When change is strictly time-specific, the total variance ($V = v_a t$) presumably would be independent of the rate of speciation and the number of species in a clade. However, as shown below, variance and number of species are correlated because clades with more species have earlier initial branch points, which contribute disproportionately to the average divergence time between species. This effect might be small if clades varied substantially in age, so that differences in the variance among clades owing to differences in age were not obscured. When change is speciation-specific, then variation in speciation rate as well as time [$V = v_c(st + 1)$] together determine variance. In this case, the product st is directly proportional to the logarithm of species number ($\ln N$), and time should not account for additional variation in the variance among clades.

In principle, phenotypic variance should always increase with time, regardless of the mechanism of phenotypic change (Slatkin, 1981). Thus, $V = v_c(st + 1) + v_a t = v_c + (v_c s + v_a)t$. Because both time-dependent and speciation-dependent change is stochastic, the actual number of either type of event within a clade within a particular time interval will vary. The number of speciation events is highly correlated with the number of species in a clade, even with random extinction (Ricklefs, 2004a), and so it is possible to estimate the realized rate of lineage formation as proportional to $\ln N$. Random variation in the number of lineages presumably breaks the correlation between speciation-dependent and time-dependent processes and should allow statistical sorting of their independent contributions to V. Accordingly, when v_c is 0, variation in $\ln N$ should be unrelated to V, except for the effect of N on average divergence time between pairs of species, and the contribution of time per se should be statistically apparent. Conversely, when v_a is 0, the realized frequency of speciation events is estimated by $\ln N$ and phenotypic variance should vary in direct proportion to this value, regardless of time. This seems reasonable, but, as we shall see, the situation is more complicated.

Simulation of Morphological Variance on Structured Phylogenies

Trait Variance is Independent of Species Number

To show that variance accumulation is independent of the number of evolving lineages, I simulated the variance among members of a clade of constant size (no speciation or extinction; equivalently, a star phylogeny), having either 10, 100, or 1000 lineages, over 24 time steps. This simulation resembles Valentine et al.'s (1994) model 2. At time 0, each lineage has a trait value of 0. At each time step, the single trait value could either increase by 1 or decrease by 1. Thus, the variance generated at each time step is 1 and the total expected variance at the end of the simulation is 24. The observed variance in these simulations was very close to the expected variance (Table 1). The observed variance also varied widely, especially for the smallest clade size, for which the distribution was also skewed significantly.

Trait Variance Depends on the Average Separation in Time between Species

I simulated morphological change over structured phylogenetic trees that were initiated with a single lineage at time 0 and produced $n = 2$, 4, or 8 species over 24

Table 1. Statistics for the observed variance (V) in simulations of character change by +1 or −1 at each of 24 time steps. The expected variance at the end of the simulation is 24; the expected standard error (StdErr) of the variance is shown in the last column (s_V).

Clade size	Trials	Mean	SD	StdErr	Min	Max	Skew	Kurt	s_V
10	1000	23.57	24.87	11.12	2.09	77.41	0.91	1.15	11.33
100	1000	23.92	24.32	3.44	15.76	36.90	0.27	−0.01	3.58
1000	1000	24.02	23.93	1.07	20.81	28.03	0.24	0.16	1.13

Note The expected standard error of the variance (s_V) is calculated according to Equation 5 in box 7.1 of Sokal and Rohlf (1995) for $V > 15$, except that $\sqrt{2n}$ should be $\sqrt{n/2}$, where n is the sample size. The variances exhibit Poisson ($n = 10$) to normal ($n = 100$, 1000) distributions.

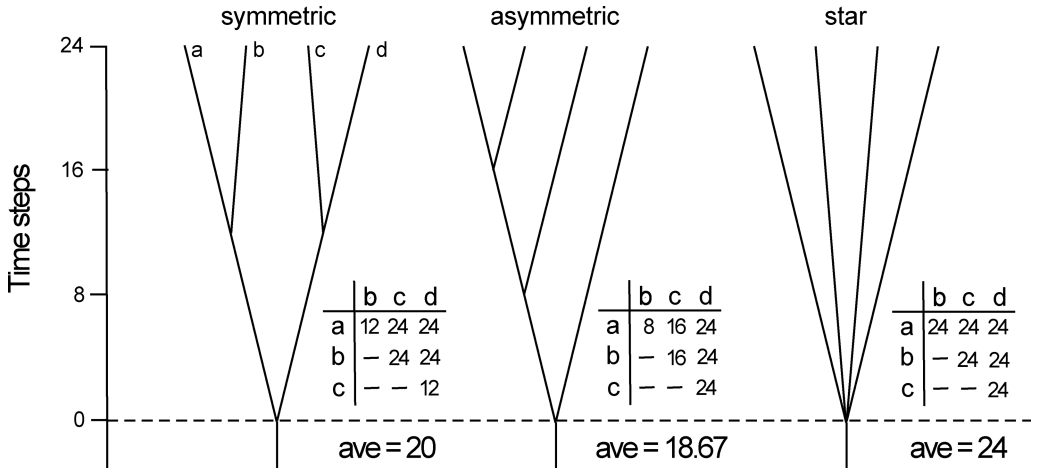

FIGURE 1. Topologies of symmetric, asymmetric, and star phylogenies for four species (a through d). The first node occurs at time 0 and simulations are run for 24 time steps. The ages of the nodes joining all pairs of species are shown for each topology in the small matrices. These ages are proportional to the expected variance generated between any two terminals, and the average of the nodal ages uniting each pair of species estimates the variance generated over each of the clades (see Table 2).

time steps. Morphological change occurred as in the previous simulation, that is, in a time-dependent fashion. Tree topology was either: symmetric, in which case lineages bifurcated at even time intervals beginning at time 0; asymmetric, in which case the phylogeny was ladder-like with $n-1$ successive branching points (nodes); or star-like, with all species diverging from a common ancestor at the base of the tree (time = 0) (Fig. 1). The initial trait value (time = 0) was 0, and morphology was incremented at the end of each time step on each branch of the phylogeny. Increments were either discrete or drawn from a continuous distribution. In simulating continuous change, the increment in the trait variable was drawn at random from a normal distribution with mean of 0 and standard deviation = 1, that is, variance increment $(v_a) = 1$. In simulating discrete change, the trait was incremented by either +1 or −1 (variance generated at each time step = 1). The expected total variance between lineages with either continuous or discrete change over 24 time steps was thus 24. When a phylogeny had internal nodes, the average divergence time between species was less than 24. Each simulation was run 10,000 times and the sample variance in trait values produced by each simulation was calculated by

$$V = \frac{1}{(n-1)} \sum_{i=1}^{n} (x_i - \bar{x})^2.$$

As shown in Table 2, the average variance obtained in phylogenies under both continuous and discrete random change conformed to the average age of the nodes separating all pairs of species in the phylogeny. Because the distribution of the variance was not normal, especially for the smaller clades (see Fig. 2), the standard deviation of the variance exceeded somewhat the value of the standard error expected from a normal distribution with variance V and sample size n.

The results of the simulations are consistent with those of Valentine et al. (1994) in that the variance in a morphological trait increases strictly as a function of time and is independent of the number of species in a phylogenetic tree. The conformation of the phylogenetic tree influences the variance only to the extent that it influences the average age of nodes uniting each pair of species in

TABLE 2. Variance obtained in trait evolution over 24 time steps on phylogenetic trees with different topologies producing two, four, or eight species. Simulations were run 10,000 times.

Species		Configuration	Pairs	Expected variance	Continuous change			Discrete change			$V/\sqrt{(n/2)}$
					Mean	SE	SD	Mean	SE	SD	
2	Star	(1,2)	1	24.00	24.03	0.34	34.00	24.21	0.33	33.39	24.00
4	Sym	((1,2),(3,4)).	6	20.00	20.17	0.19	19.08	20.13	0.19	18.51	14.14
4	Asym	(1,(2,(3,4)))	6	18.67	18.32	0.17	16.64	18.43	0.16	16.24	13.20
4	Star	(1,2,3,4)	6	24.00	23.84	0.02	19.59	23.69	0.19	19.09	16.97
8	Sym	(((1,2),(3,4)),((5,6),(7,8)))	28	19.43	19.39	0.14	13.84	19.48	0.13	13.23	9.71
8	Asym	(1,(2,(3,(4,(5,(6,(7,8)))))))	28	18.00	17.99	0.11	10.81	17.76	0.10	10.29	9.00
8	Star	(1,2,3,4,5,6,7,8)	28	24.00	24.02	0.13	12.92	24.08	0.13	12.86	12.00

Note. The expected variance is the average age of the node uniting all pairs of species in the clade. The total branch length in each of the phylogenies is 2 species star = 48; 4 sym = 72; 4 asym = 72; 4 star = 96; 8 sym = 112; 8 asym = 129; 8 star = 192.

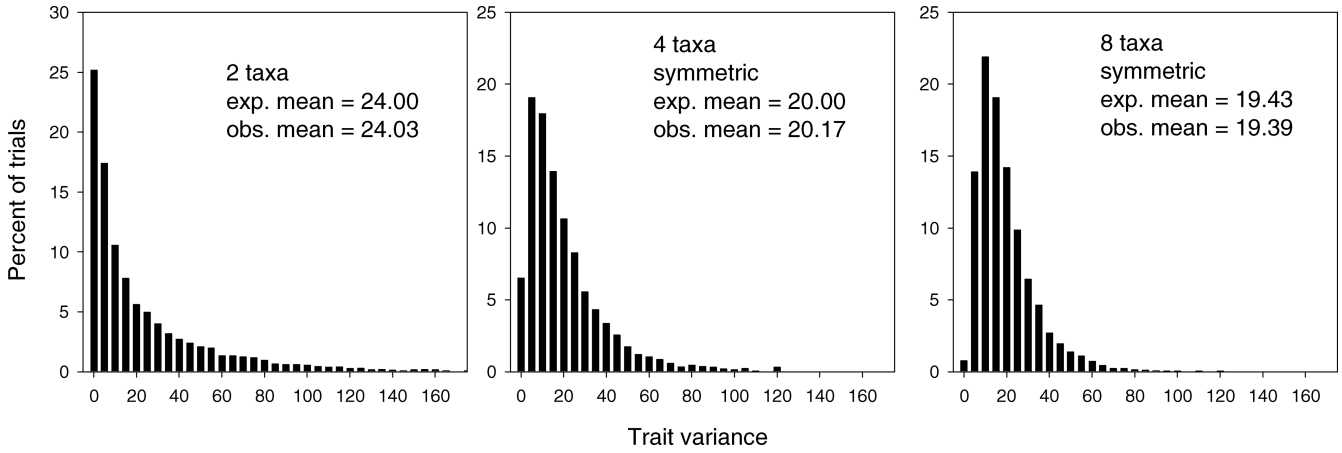

FIGURE 2. Distribution of variance over 10,000 simulation trials when morphological variance increments by an average of 1 unit over 24 time steps over clades of two, four, and eight species having symmetric topology (see Fig. 1).

the phylogeny. This effect can be large, however, leading to a correlation between variance and number of species.

The predicted variance from time-dependent and speciation-dependent trait change is identical when the time-dependent variance increment equals the product of the speciation rate and the speciation-dependent variance increment. This identity holds because in a speciation-dependent process, the variance is proportional to the average number of nodes separating each pair of species in a clade, which is directly proportional to the average age of the nodes uniting each pair of species (see, for example, Wagner, 1997). Under speciation-dependent change and assuming no extinction, the number of species is an exponential function of the product of the speciation rate and time, that is $N = e^{st}$, and the speciation rate is therefore proportional to the logarithm of the number of species. Even with extinction, the logarithm of the number of speciation events is strongly related to the logarithm of the number of species (Ricklefs, 2004a, Methods).

SIMULATING RANDOM TRAIT VARIATION OVER RANDOMLY GENERATED PHYLOGENIES

To explore Purvis's (2004) contention that time-dependent and speciation-dependent diversification cannot be distinguished by multiple regression of variance on the age of a clade and the logarithm of the number of species, I simulated change in a morphological trait on randomly generated phylogenies. The simulations were performed using a MatLab scrip "Morphtreegen" written by Brian Sidlauskas. The simulations incorporated random speciation and extinction and random time-dependent or speciation-dependent morphological change. The output included the ages of nodes within each tree and trait values for terminals of both extinct and extant lineages. In the present simulations, all trait changes were drawn from random normal distributions with mean 0 and variance 1. At speciation events, only one lineage (the "parent lineage") was subject to change, regardless of whether change was time-dependent or speciation-dependent. I calculated the variance in trait values among extant lineages, but could not easily recover the matrix of distances among pairs of species from the output. Accordingly, I conducted parallel simulations using PhyloGen, version 1.1, developed by Andrew Rambaut (http://evolve.zoo.ox.ac.uk/software/PhyloGen/main.html), to produce phylogenetic trees from which one could calculate the average age of nodes uniting all pairs of extant species. Stephen B. Heard kindly converted the Newick format outputs from these simulations to distance matrices. Occasional negative branch lengths produced by PhyloGen were left unchanged.

Six simulations were designed to (1) replicate Purvis's time-constant simulation; (2) produce smaller clades in the same time-constant simulation to test the effect of total branch length; (3) replicate Purvis's species-constant simulation; (4) use the same parameters but vary time as well as the number of species in a clade; (5) create an extreme uncoupling of clade duration and speciation rate; and (6) simulate speciation-dependent change.

Time-dependent trait change, constant time (simulation 1).—I simulated morphological change over 25 trees using the same parameters as in Purvis's (2004) first simulation: 60 time steps, speciation rate (s) = 0.20, extinction rate (e) = 0.16 (80% of the speciation rate), time-dependent morphological change drawn from a normal distribution with mean = 0 and variance = 1. The expected extant clade size is $N = (se^{(s-e)t} - e)/(s - e) = 51.1$ terminals (see Ricklefs, 2003). The average number of species in the simulation was 47.2 ± 39.6 SD (range, 2–158). The average variance generated within clades was 29.5 ± 23.5 SD units^2, i.e., equivalent to about half the total time duration. Morphological variance was strongly correlated with log-number of species ($\log N$), with a slope of 24.5 ± 7.0 SE ($F_{1,23} = 12.3$, $P = 0.002$, $R^2 = 0.348$), in spite of trait variance being generated by a time-dependent process.

To determine whether the relationship between variance and number of species resulted from a greater average distance between pairs of species in larger clades, I used PhyloGen to generate 25 random trees with the same parameters: $s = 0.20$ and $e = 0.16$ over 60 time steps. The average number of species was 50.9 ± 34.3 SD (5–100), and average distance within clades was 29.1 ± 10.0 SD. These values are almost identical to the number of species and variance generated in the previous simulation. The broader distribution of variances in the trait simulations (SD = 23.5 versus 10.0) can be attributed to the variance added by stochastic morphological change. The relationship between average distance and log$N$ had a slope of 18.5 ± 3.6 SE ($F_{1,23} = 26.2$, $R^2 = 0.512$), which did not differ significantly from the slope obtained between the variance and log$N$ in the previous simulation. The maximum nodal age, i.e., the base of the crown group, averaged 43.0 ± 12.5 SD time steps.

Time-dependent trait change, constant time, no extinction (simulation 2).—I ran 25 simulations as above; however, speciation rate was set at 0.04 and extinction rate at 0.00, yielding the same net proliferation rate (0.04) and an expected clade size ($N = e^{st}$) of 11.0. Number of terminals per simulated clade averaged 11.4 ± 10.1 SD (2–39). The average variance within clades was 25.7 ± 22.5 SD units^2, i.e., similar to the value obtained under a higher turnover rate and larger extant clade size. This is significant because the first simulation had many more speciation events, more species, and more total branch length in each clade. Morphological variance in the smaller clades in simulation 2 was strongly correlated with log$N$ ($r = 0.64$, $P = 0.0006$), with a slope of 36.1 ± 9.1 SE ($F_{1,23} = 15.7$, $P = 0.0006$, $R^2 = 0.405$).

A parallel set of 25 phylogenies was simulated in PhyloGen using the same parameters. The number of terminals per simulated clade averaged 11.8 ± 8.4 SD (3–42). The average age of nodes uniting species was 29.2 ± 11.5 SD units^2, and age increased with log species number with a slope of 32.0 ± 5.1 SE ($F_{1,23} = 39.1$, $P < 0.001$, $R^2 = 0.614$). The maximum nodal age averaged 42.1 ± 12.5 SD time units.

Time-dependent trait change, constant clade size (simulation 3).—I simulated 25 trees under the same conditions used by Purvis (2004) in his second example (speciation rate = 0.20, extinction rate = 0.16; time unlimited but simulations terminated after 50 species had been produced). In this case, the simulation with Morphtreegen continued through the time interval during which the 50th species appeared, and so the clades typically had more than 50 species (51–61). Durations of the simulations averaged 73.0 ± 21.4 SD (34–114) time steps, and trait variance averaged 26.1 ± 18.0 SD units^2. Morphological variance was not correlated either with (not surprisingly) log$N$ ($r = 0.135$, $P = 0.520$) or with the duration of the simulation ($r = 0.107$, $P = 0.610$). The average variance within clades did not differ from the simulations over a fixed interval.

A parallel set of 25 phylogenies was produced in PhyloGen using the same parameters. In this case, the average ages of nodes uniting pairs of species averaged 32.4 ± 9.8 SD. The smaller variation among ages within clades might reflect the constant number of species generated. The maximum age averaged 47.9 ± 17.1 time units. Because the number of species was approximately constant, the relationship between average age and species number is not applicable.

Time-dependent trait change, constant net diversification rate, variable clade duration (simulation 4).—To determine whether variation in clade age would break the correlation between variance and log$N$ in a time-dependent process, as I suggested (Ricklefs, 2004b) in my response to Purvis (2004), I performed 35 simulations with $s = 0.20$ and $e = 0.16$: five at each of 25, 35, 45, 55, 65, 75, and 85 time steps. Variance, log$N$, and duration were intercorrelated (V-log$N$, $r = 0.531$, $P = 0.0010$; V-duration, $r = 0.406$, $P = 0.016$; log$N$-duration, $r = 0.602$, $P = 0.0001$). In a multiple regression, variance was uniquely related only to log$N$ ($F_{1,32} = 5.83$, $P = 0.022$, slope = 26.4 ± 10.9). When three outlying values ($V > 80$) were deleted, the correlation of V with log$N$ increased to 0.718 ($P < 0.0001$, $n = 32$), duration was not significant in a multiple regression, and the slope of V on log$N$ was 17.2 ± 3.9 ($F_{1,31} = 15.4$, $P < 0.0001$, $R^2 = 0.515$).

A parallel set of 35 phylogenies was produced in PhyloGen using the same parameters. The terminals per simulated clade averaged 37.4 ± 31.0 (2–101) SD. The average age of nodes uniting species was 24.2 ± 15.7 SD units^2. Average distance, log$N$, and duration were intercorrelated (dist-log$N$, $r = 0.839$, $P < 0.0001$; dist-duration, $r = 0.781$, $P < 0.0001$; log$N$-duration, $r = 0.710$, $P < 0.0001$). In a multiple regression, distance was related to log$N$ ($F_{1,32} = 23.0$, $P < 0.0001$) with slope 18.2 ± 3.8 and to duration ($F_{1,32} = 9.8$, $P = 0.0037$) with slope 0.289 ± 0.092 per time step (overall model $F_{2,32} = 54.5$, $P < 0.0001$, $R^2 = 0.773$). Evidently, varying duration more than threefold does not erode the strong correlation between the average age of nodes and number of species. Thus, contrary to the assertion in my response to Purvis (2004), for a given speciation-extinction process, the average age of nodes is better predicted by the number of contemporary species than by the age of the clade.

Time-dependent trait change, diversification rate × duration constant (simulation 5).—These simulations have the same expected number of species regardless of duration, and one would expect, therefore, that the average age of nodes uniting species would be proportional to duration. Accordingly, with time-dependent trait change, both time and number of species should significantly affect the variance generated. I ran 35 simulations, including 5 each at durations of 24, 30, 40, 48, 60, 72, and 80 time steps, with speciation rate × time = 12, and extinction rate = 0.80× speciation rate. The important result here is that log$N$ and duration were uncoupled ($r = 0.209$, $P = 0.227$) and V was independently

TABLE 3. Properties and results of six simulations of random morphological diversification over randomly generated phylogenetic trees.

	Simulation					
	1	2	3	4	5	6
Clades (n)	25	25	25	35	35	35
Variance dependence	Time	Time	Time	Time	Time	Speciation
Stop criterion	Time	Time	Species	Time	Time	Time
Time steps	60	60	34–114	25–85	24–80	24–80
Speciation rate (s)	0.20	0.04	0.20	0.20	12/time	0.20
Extinction rate (e)	0.16	0.00	0.16	0.16	$0.8 \times s$	0.16
Expected species (N)	51.1	11.0	50	57.0	51.1	48.3
Observed species	47.2	11.4	—	46.3	48.3	43.4
SD	39.6	10.1	—	56.6	43.7	44.9
Trait variance (V)	29.5	25.7	26.1	23.6	21.4	5.20
SD	23.5	22.5	18.0	28.0	21.8	4.64
Regression of V on log$N$, slope	24.5	36.1	NA	26.4	24.4	—
SE of slope	7.0	9.1	—	10.9	5.9	—
Regression of V on time, slope	NA	NA	NS	NS	0.456	0.123
SE of slope	—	—	—	—	0.137	0.035
Ages of nodes generated by Phylogen						
Observed species	50.9	11.8	NA	37.4	Not done	Not done
SD	34.3	8.4	—	31.1	—	—
Average age of nodes	29.1	29.2	32.4	24.2	—	—
SD	10.0	11.5	9.8	15.7	—	—
Regression of age on log$N$, slope	18.5	32.0	NA	18.2	—	—
SE of slope	3.6	5.1	—	3.8	—	—
Regression of age on time, slope	NA	NA	NS	0.289	—	—
SE of slope	—	—	—	0.092	—	—

related to log$N$ ($r = 0.603$, $P < 0.0001$) and duration ($r = 0.522$, $P = 0.0013$). In a multiple regression, both duration (slope $= 0.456 \pm 0.137$, $F_{1,32} = 11.1$, $P = 0.0022$) and log$N$ (slope $= 24.4 \pm 5.9$, $F_{1,32} = 17.25$, $P = 0.0002$) contributed to the variance ($F_{2,32} = 17.9$, $P < 0.0001$, $R^2 = 0.528$). Thus, one finally can demonstrate that variance bears a unique relationship to clade age in a time-dependent process, but only under the unlikely condition of an inverse relationship between speciation rate and clade age and with a continuing statistical relationship to clade size.

Speciation-dependent trait change, variable duration (simulation 6).—When trait change is speciation-dependent, one would expect variance to be related simply to log$N$, and not to time. I simulated a speciation rate of 0.20 and an extinction rate of 0.16, including five trials each of durations of 24, 30, 40, 48, 60, 72, 80 time units, as in simulation 5. Morphology changed only at speciation and only in the mother lineage. Thus, each speciation event generates 0.5 units of variance, on average, between lineages. The logarithm of the number of species was strongly related to duration ($r = 0.675$, $P < 0.0001$), as one would expect, and variance was related to both log$N$ ($r = 0.439$, $P = 0.0084$) and duration ($r = 0.527$, $P = 0.0011$). In a multiple regression, only duration was uniquely significant ($F_{2,32} = 4.4$, $P = 0.043$); however, most of the variation in the variance was related to correlated effects of duration and log$N$, which cannot be separated statistically. In a regression with only duration, the slope of V with respect to time was 0.123 ± 0.035 ($F_{1,33} = 12.7$, $P = 0.0011$, $R^2 = 0.278$), which was close to the prediction of half the rate of speciation.

SIMULATION RESULTS SUMMARIZED

The results of the six simulations are summarized in Table 3. The standard deviations of the number of species and the trait variance over trials are approximately equal to the means, which is consistent with the geometric distributions expected from random Bernoulli trials. The results of these simulations confirm the following relationships concerning trait variance. First, in both time-dependent and speciation-dependent processes trait variance is proportional to the age of the node uniting two species. Thus, the trait variance within a clade is equal to the average age of nodes uniting all pairs of species in the clade. Variance does not depend on number of species or total branch length in a phylogeny. For example, in simulation 2, where speciation rate was greatly reduced without changing the net proliferation rate (speciation − extinction), resulting in a fivefold reduction in the number of species, the trait variance as well as the average age of nodes was unchanged.

Second, in a time-dependent process of trait change, the logarithm of the number of species in a clade is a better predictor of the average age of nodes uniting species than the age of the clade (including its stem). Even when clade age varies more than three-fold, as in simulation 4, log$N$ provides a better estimate of average nodal age than does the age of the clade. The same was true for the maximum node age (i.e., the first branch point among extant species), which increased by 27.2 ± 5.1 SE time units per $\log_{10}$ unit of species number ($F_{1,32} = 28.2$, $P < 0.0001$) and much more weakly, by 0.321 ± 0.124 SE time units per unit of clade age ($F_{1,32} = 6.7$, $P = 0.015$). Thus, the average nodal age uniting extant species in a clade is

retrospective and mostly unrelated to the age of a clade from its base. Even the base of the crown group (maximum node age) was better predicted by the number of species than by clade age.

Third, when trait change is speciation-dependent, number of species and time are so closely related that neither uniquely predicts the trait variance generated. Thus, regressions of trait variance on clade age or log$N$ cannot distinguish between mechanisms of trait change. Missing from the analyses presented here, because simulations were split between two programs, is the relationship between trait variance and average pairwise distance within clades.

Partitioning Time-Dependent and Speciation-Dependent Random Evolution

Because anagenesis and cladogenesis both predict that morphological variance should be related to the number of species in a clade, distinguishing the two modes of evolution statistically presents a difficult challenge, as Purvis (2004) suggested. Indeed, the logarithm of the number of species could provide a better estimate than clade age of the trait variance under both modes of evolution because species number estimates both the average age of nodes uniting species in a phylogeny and the realized number of speciation events.

If both time (that is, average pairwise divergence time) and number of species in a clade varied independently, as they might when speciation and extinction are random processes, variance could be partitioned by multiple regression–partial correlation into a time-dependent component, a speciation-dependent component, and a third component associated with the correlated variation in the two. This analysis approach would require complete phylogenies of clades to calculate average ages of nodes uniting species, and these are presently available for too few groups to perform such an analysis. Moreover, I was not able to perform simulations that would have shown whether this approach might be useful.

Clearly, the greater the independence of time and species—that is, the lower their correlation—the larger the proportion of the trait variance that can be associated with one or the other mechanism. The relevant simulation here is number 4, with clade age varying by a factor of more than 3; however, in this case, time was still not a significant predictor of variance when log$N$ was included, and was only a weak predictor of average age of nodes uniting species. When speciation and extinction rates are homogeneous among clades, there does not appear to be enough variation in clade duration to break the correlation between nodal age and number of species, especially recalling that the logarithm of the number of species is also approximately proportional to time.

A possibility for statistical partitioning of time-dependent and speciation-dependent change would seem to exist in samples of clades in which both clade age and the rate of speciation vary. However, even when age and speciation rate were inversely related to each other in simulation 5, log$N$ remained a better predictor of V than clade age. Moreover, without knowing the rate of extinction, one cannot estimate the rate of speciation from the rate of branching in the phylogenetic tree of extant species. Nee et al. (1992) and Harvey et al. (1994) have shown that the rates of speciation and extinction can be estimated from lineage-through-time plots (see also Ricklefs, 2006). These estimates depend, however, on rate homogeneity over time, which is probably rarely the case (Heard, 1996), and in any event estimates for small clades would have broad confidence limits.

Time-dependent change along a particular branch in a phylogeny is proportional to its length, whereas speciation-dependent change is not. Thus, when one can estimate the length and morphological change for each branch in a phylogeny it should be possible to distinguish between these modes of morphological change by the presence or absence of a correlation between the two (Pagel, 1999). However, this approach relies on estimates of branch lengths and trait values for ancestral nodes within a phylogeny, both of which typically have broad confidence limits (Schluter et al., 1997; Felsenstein, 2004; Ronquist, 2004), and assumes an absence of cryptic speciation along branches, i.e., no extinction. Furthermore, although rates of morphological and molecular evolution might be generally uncoupled (Bromham et al., 2002), the apparent correlation between speciation events and molecular phylogenetic branch lengths (Webster et al., 2003) raises concerns about using branch lengths to estimate time.

In conclusion, my analysis of the relationship of trait variance to age and number of species in clades (Ricklefs, 2004a) could not distinguish between time-dependent and speciation-dependent processes (Purvis, 2004), and my statement that trait change was speciation-dependent is not supported. Potential further development of this approach should be based on estimates of nodal age within clades rather than clade age itself. Other phylogeny-based approaches (e.g., Mooers et al., 1999; Pagel, 1999; e.g., Bokma, 2002) also will not likely perform well because of uncertainties concerning extinction events, broad confidence limits on estimates of branch lengths and ancestral trait values, and the strong correlation between divergence time and species number in proliferating clades.

As an alternative, rapid speciation-dependent morphological change could be tested by comparison of morphological divergence between allopatric populations of recent derivation and sympatric sister taxa, particularly in archipelagoes where new populations typically arise from small numbers of colonists (the peripatric model of species formation: Mayr, 1963; Carson and Templeton, 1984; Coyne and Orr, 2004). The role of species interactions in time-dependent morphological change could be assessed by comparing the relationship between morphological divergence and time (genetic divergence) in

allopatric and sympatric sister taxa, assuming that sister taxa would exert stronger diversifying selection than the unrelated species encountered in a newly colonized region. If diversifying selection imposed by interactions between close relatives were the driving force in morphological change, then the number of species in a clade would directly influence morphological variance. If divergence were slow relative to species formation, then total branch length within a clade might also contribute to morphological variance. The results presented here apply only to models of random morphological change. Clearly, the natural world is more structured than this.

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