PATTERNS IN PHYLOGENETIC TREE BALANCE WITH VARIABLE AND EVOLVING SPECIATION RATES

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Abstract.—Aspects of phylogenetic tree shape and in particular tree balance provide clues to the workings of the macroevolutionary process I use a simulation approach to explore patterns in tree balance for several models of the evolutionary process under which speciation rates vary through the history of diversifying clades I demonstrate that when speciation rates depend on an evolving trait of individuals, and are therefore "heritable" along evolutionary lineages, the resulting phylogenies become imbalanced. However, imbalance also results from some (but not all) models of "nonheritable" speciation rate variation. The degree of imbalance increases with the magnitude of speciation rate variation, and then for gradual evolution (but not punctuated equilibria) reaches an asymptote short of the theoretical maximum Very high levels of rate variation are required to produce imbalance matching that found in real data (estimated phylogenies from the systematic literature) I discuss implications of the simulation results for our understanding of macroevolution

Key words —Macroevolution. phylogenetic trees, punctuated equilibria. speciation rates tree balance, tree topology

The topology of every phylogenetic tree reflects, at least in part, the evolutionary processes that produced it One aspect of phylogenetic tree topology that has attracted much recent attention (Mooers and Heard in press) is tree balance—the extent to which branch points define subgroups of equal size (Fig 1). Balance is an interesting property of phylogenetic trees because it has been associated with variation in speciation or extinction rates among lineages within a larger clade (Savage 1983; Guyer and Slowinski 1991; Heard 1992): more rate variation is said to produce more imbalanced trees Such rate variation has been implicated in important macroevolutionary phenomena, including species sorting (Vrba 1980, 1984; Vrba and Eldredge 1984; Eldredge 1989), key innovation and adaptive radiation (Guyer and Slowinski 1993; Slowinski and Guyer 1993; Heard and Hauser 1995), and biogeographical controls on diversification (Jablonski et al 1983). If balance provides an accurate measure of past variation in speciation and extinction rates, studies of balance could make major contributions to our understanding of macroevolutionary dynamics (Savage 1983; Heard 1992; Guyer and Slowinski 1993; Kirkpatrick and Slatkin 1993)

Estimated phylogenetic trees (cladograms and phenograms) tend to be more imbalanced than expected under an equal-rate, random speciation model (the "Markov model"; Guyer and Slowinski 1991; Heard 1992; Mooers 1995; Mooers and Heard in press), and this tendency is independent of methodological details of the trees' estimation (Heard 1992; Heard and Mooers 1996) The existence of such imbalance suggests that speciation or extinction rates have, in fact, been variable in many or most clades However, the consequences (for balance) of different patterns in speciation and extinction rates have not been explored Without some understanding of the effects of simple kinds of rate variation on tree balance, it will be difficult to interpret the balance or imbalance of estimated trees.

A particularly interesting form of variation in speciation or extinction rates is that resulting from the dependence of these rates on evolving traits of individuals For example,

speciation rates might depend on body size (Kochmer and Wagner 1988; Reaka-Kudla 1991) if (among many possible mechanisms) smaller organisms have faster generation times or smaller and more easily subdivided geographical ranges (Peters 1983) Speciation-rate variation arising in this way can be thought of as heritable within lineages, as parent and daughter species will resemble one another in speciation rate (or, equivalently, speciation probability) by virtue of their resemblance in trait value This kind of speciation rate variation drives species sorting (Vrba 1980, 1984; Vrba and Eldredge 1984; Eldredge 1989) and is the basis of key innovation hypotheses (Heard and Hauser 1995) Even if this trait-based kind of rate variation has been common, however, it has likely been accompanied by rate variation unrelated to heritable organismal traits—for instance, variation stemming from climate change, from vicariance, or from changes in competitive interactions I will use the terms "heritable" and "nonheritable" in referring to speciation rate components passed and not passed, respectively, from ancestor to descendent species in a lineage These different rate components could have very different effects on tree balance

In this paper, I use simulation modeling to examine the tree-balance consequences of speciation-rate variation under several different evolutionary models. I seek to answer three basic questions First, which kinds of speciation-rate variation affect balance, and which do not? Second, how sensitive is balance to the magnitude of speciation-rate variation? Finally, is balance affected strongly enough that speciation-rate variation can account for the imbalance seen in samples of estimated trees (Guyer and Slowinski 1991; Heard 1992; Mooers 1995)?

METHODS

I used a computer program written in QuickBASIC to simulate branching evolution under various evolutionary scenarios (Table 1) These scenarios differed in assumptions about the evolutionary process and in the magnitudes of evo-
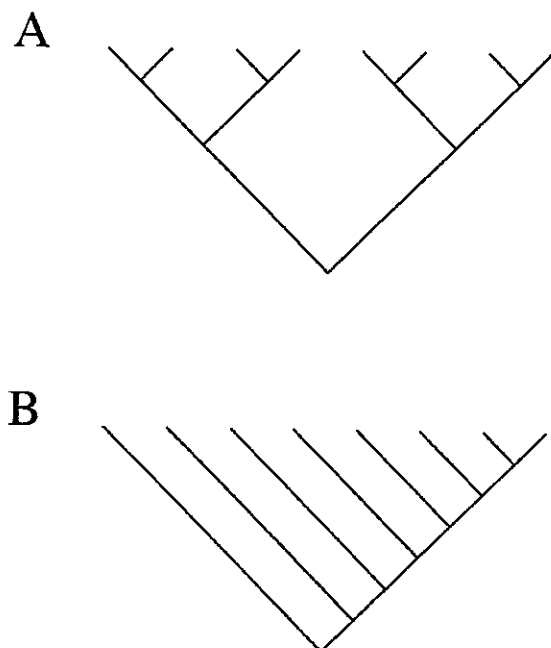
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A

B

FIG 1. Perfectly balanced (A) and imbalanced (B) eight-taxon phylogenetic trees Tree (A) has $I = 0$; tree (B) has $I = 1$.

lutionary rates; I defer full coverage of these differences to the description of the computer algorithm

All the scenarios I examined shared the following basic features. I simulated the evolution of clades beginning with a single ancestral species, as those clades diversified through time to a preset target size In all cases, I allowed speciation rates (or probabilities) to depend on a quantitative trait of

individuals that was evolving in a random walk. Therefore, these rates changed through time and differed among the species present at any instant in a growing tree. Speciation rates were also allowed to vary among species in ways unrelated to any evolving trait My focus was on patterns in balance of the resulting trees

The Computer Algorithm

My algorithm generated each tree by beginning with a single species, and then stepping through time allowing both trait evolution and speciation events until the tree reached the desired size At each time step, each of the species in the growing tree had two associated quantities (Fig. 2): a value x for a quantitative trait (such as body size), and a (relative) speciation rate s, which is some function of x Three interdependent processes are therefore involved in the simulated evolutionary history: evolutionary change in trait values, the conversion of trait values to speciation rates, and speciation itself

Trait Evolution.—The modeled quantitative trait could represent any continuous characteristic of individuals that is associated with speciation rate; body size is one obvious possibility I used three models for determining the size of trait value changes (Table 1A). In all three, at each opportunity for change (see below) a lineage "inherited" the trait value it held previously, plus some stochastic change The models differed in exactly how this stochastic component was calculated

In the first model, trait evolution followed a log-Brownian motion model: at each opportunity for trait evolution (see below), the logarithm of the new trait value was simply the logarithm of the old value plus a change (ϵ_x) drawn from a normal distribution with expectation zero and standard de-

TABLE 1. Evolutionary models used in simulations Setting up an evolutionary scenario for a simulation run involves choosing one option from each of (A) (B) and (C).

(A) Size of trait value changes Model	New trait value[a]	Bounds on trait value
Log-Brownian *or*	$\log(x_{new}) = \log(x_{old}) + \epsilon_x$	$(0, +\infty)$
Linear-Brownian *or*	$x_{new} = x_{old} + \epsilon_x$	$(0, +\infty)$
Linear-Brownian bounded	$x_{new} = x_{old} + \epsilon_x$	$(0, 20)$

[a] Transformation applied at each trait value change In all cases ϵ_x is a normally distributed random variable with expectation zero and standard deviation σ_x

(B) Timing of trait value changes Model	Trait value change	
Punctuated *or*	in one daughter, at speciation events	
Gradual	at every time step	

(C) Noise used to determine relative speciation rates Model	Speciation rate function[b]	Timing of recalculation[c]
Intermittent *or*	$s = 10^{\log(x) + \epsilon_s}$	only when x changes
Continuous	$s = 10^{\log(x) + \epsilon_s}$	every iteration

[b] ϵ_x is a normally distributed random variable with expectation 0 and standard deviation σ_s
[c] The two models are indistinguishable under the gradual model for trait value changes

time 2

$x = 11.2; s = 13.5$

$x = 14.8; s = 14.2$

$x = 10; s = 9.1$

time 1

$x = 11.2; s = 13.5$

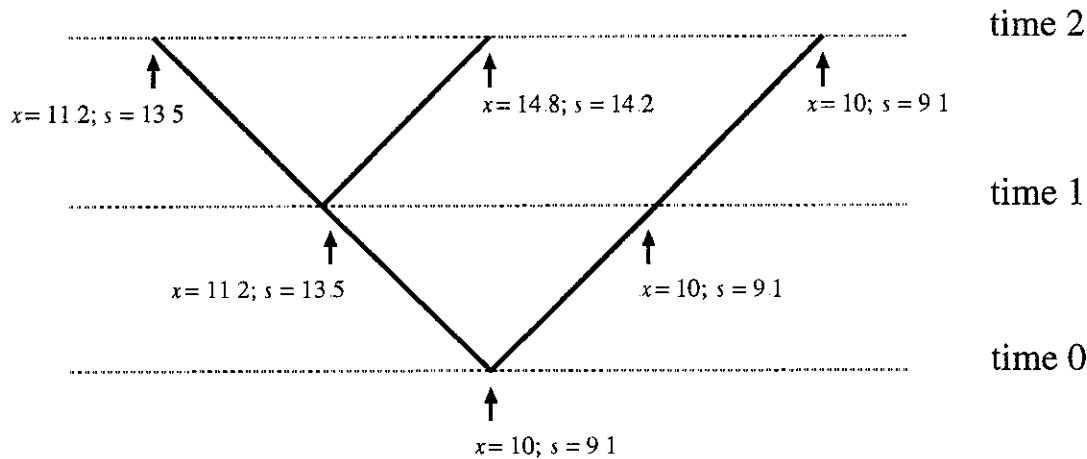$x = 10; s = 9.1$

time 0

$x = 10; s = 9.1$

FIG. 2. A growing phylogenetic tree. Dashed lines represent time steps (iterations) in the computer model. At each time step, each species has a trait value x and a (relative) speciation rate s. Shown is one possible case when $\sigma_x = \sigma_s = 0.1$, and trait evolution is punctuated and log-Brownian (Table 1).

viation σ_x. The starting value of x for each tree was (arbitrarily) 10. The log values were not bounded, and so the x-values have the range $(0, +\infty)$. Under the log-Brownian model, evolutionary change was additive on a logarithmic scale: a given *proportional* change in trait value was equally likely for any current trait value, but a given *absolute* change was not.

The second model for trait evolution was a linear-Brownian model, where additive changes were made to the trait value instead of its logarithm (Felsenstein 1985; Martins and Garland 1991). Trait values were restricted positive (by truncation), but unbounded above.

The third model was again linear-Brownian, but restricted the trait values (again by truncation) to a symmetrical interval about the starting value: (0, 20). In all three models, the new trait value was a function of the old trait value and the stochastic change ϵ_x. In no case was the direction of evolution biased, although when speciation rate was tied to trait values, large trait values accumulated by a process of species sorting.

Of the three models for trait value change, I expect that the log-Brownian is the most realistic. This is because, for instance, a 1 kg increase in body mass might be trivial in a clade of vertebrate carnivores, but utterly preposterous among dragonflies. A 10% increase in body mass, on the other hand, might be equally plausible for either group, and this is how the log-Brownian model behaves.

The timing of changes in trait value depended on the evolutionary model (Table 1B). Under a gradual model, trait values changed at every time step. Under the punctuated model, trait values changed only at speciation events, with one of the daughter species taking a new trait value. The one-daughter-changes punctuated model is that expected (Eldredge and Gould 1972) from an allopatric-speciation model where most evolutionary change occurs in the small, peripheral isolates that produce new species. It might also be possible, if less plausible, for both daughter species to undergo trait evolution at speciation events (Smith 1983). A two-daughters-change punctuated model showed very similar be-

havior to the one-daughter-changes model and I discuss it no further here.

Speciation Rates.—Speciation was a stochastic process, with the relative speciation rate for any extant lineage at any iteration represented by s. The rate s in turn was a function of the trait value x and a "noise" component ϵ_s, drawn from a normal distribution with expectation zero and standard deviation σ_s (Table 1C). The dependence of s on x is analogous to the log-Brownian model for trait evolution, in that it modeled proportional changes and was not biased in direction.

While x evolved and was therefore heritable along lineages, ϵ_s was not, because it was discarded and a new term drawn to recompute s from x whenever a speciation rate was calculated. Speciation rates therefore had a heritable component (x) and a nonheritable component (ϵ_s), analogous to the heritable and nonheritable components of individual-level traits.

There were two models for the speciation-rate calculations (Table 1C). Under the "intermittent" model, a new speciation rate was calculated only when the trait value was allowed to change (when σ_x was zero, the trait value was still "allowed to change" even though all changes were zero). Variation of this sort might result, for instance, when vicariance drives speciation and the resulting geographic separation of daughter taxa confers differences in subsequent extinction or speciation rates (Kirkpatrick and Slatkin 1993).

Under the "continuous" model, in contrast, a new ϵ_s was drawn, and speciation rate recalculated, at every iteration whether or not there had been an evolutionary change in the trait value. Here ϵ_s represented factors such as climate or competitors, which affect speciation and extinction rates but could act continuously and independently of the evolutionary history of the lineage.

Note that under gradual trait evolution, the intermittent- and continuous-noise models are equivalent. When $\sigma_s = 0$, speciation rate is entirely determined by the quantitative trait x. Also, when $\sigma_x = \sigma_s = 0$, we have the equal speciation rates (Markov) null model, the behavior of which is known analytically (Heard 1992; for this special case, my simulation

procedure produced imbalance indices matching the analytical expectation)

Speciation —At each iteration, each extant species was allowed to speciate with a probability proportional to its relative speciation rate s. The s-values were converted to probabilities at each iteration by dividing each s by a common factor f chosen such that $\Sigma s/f$ was 0 01 This was equivalent to adjusting the length of the iteration time step to largely prevent multiple speciation events in the same time step Under gradual trait evolution and for continuous noise (Table 1), however, using shorter time steps meant more opportunities for evolution to act and therefore could have allowed more rapid change in x and s. To compensate for this effect, offsetting corrections were made to rates of trait evolution (σ_x) and speciation rate noise (σ_s). For instance, if f doubled (halving speciation probabilities per time step), σ_x and σ_s would each be divided by $\sqrt{2}$ to give the same net rate of change This means that the behavior of the model is completely independent of the (arbitrary) choice of time step for iteration

Average s and x increased with time by species sorting (see Vrba and Eldredge 1984; Eldredge 1989) Iteration was continued until the tree reached the target size, with a very few trees exceeding the target being discarded I did not continue the simulation to include an interval between the last speciation event and our observation of the tree, as would exist for a real tree. Because the model did not allow extinction of a lineage once it is formed (that is, extinction was included only insofar as s is a *net* speciation rate), and because I analyzed tree topologies and not distributions of trait values, the omission of such an interval made no difference to the results

Analysis

Under each scenario I generated 2000 trees, each of size 4, 6, 8, 10, 15, 20, 25, 30, 40, and 50 species For each tree, the computer program calculated and recorded Colless' index of imbalance, I (Colless 1982; called C by Kirkpatrick and Slatkin 1993):

$$I = \frac{\sum\limits_{\text{(all interior nodes)}} |T_R - T_L|}{(n - 1)(n - 2)/2}, \qquad (1)$$

where the tree has n tips (for instance, species) and at any node the right- and left-hand branches subtend T_R and T_L tips I ranges from zero for a perfectly balanced tree to one for a perfectly imbalanced tree (Fig 1). The expectation for I, under the equal speciation rates (Markov) null model, has been derived analytically and depends on tree size (Heard 1992; Rogers 1994; see bottom curve in Fig 3)

The program also calculated two other imbalance measures: σ^2_N and B_1; σ^2_N is the variance in the number of nodes between the terminal taxa and root of a tree (Sackin 1972) B_1 is the sum, over all nodes except the root, of the maximum number of other nodes between that node and its terminal taxa (Shao and Sokal 1990) I, σ^2_N, and B_1 performed very
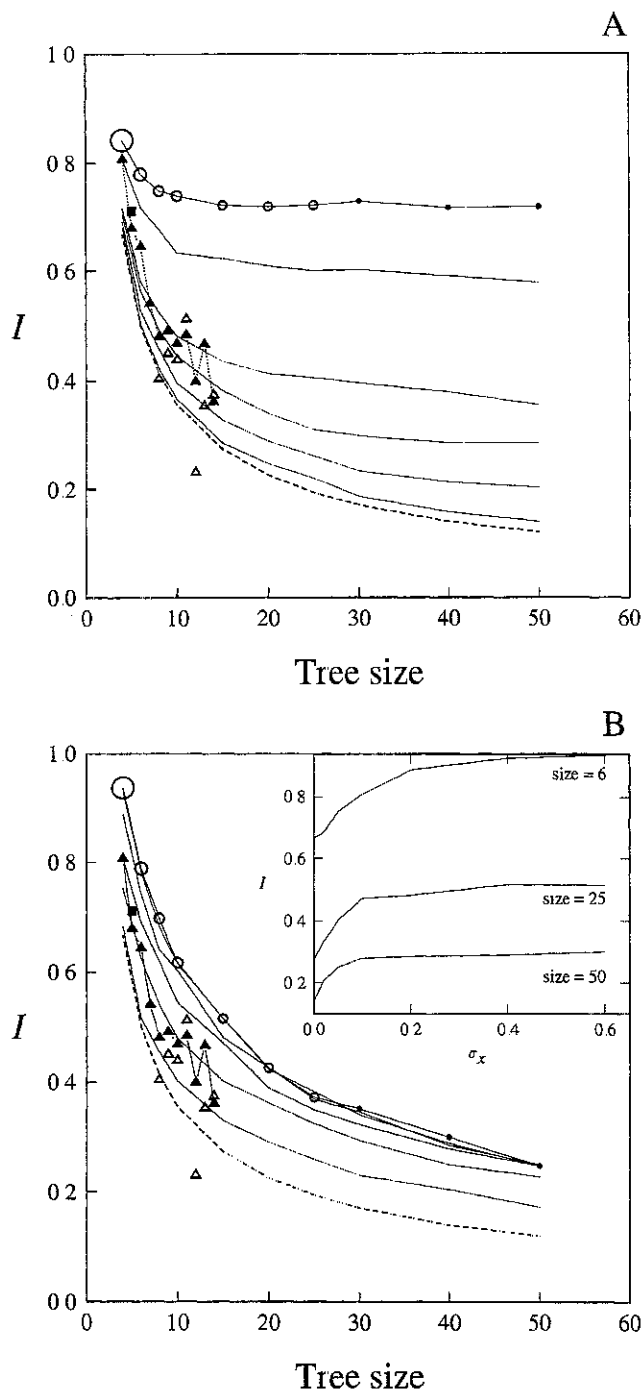

FIG 3. Imbalance for simulated phylogenies with speciation rates depending entirely on the quantitative trait x ($\sigma_x > 0$, $\sigma_s = 0$; log-Brownian changes) The lower dashed line is the Markov equal-rate expectation ($\sigma_x = \sigma_s = 0$) Hollow circles cover 95% confidence intervals (mean $\pm$ 2 SE) around simulation results. Triangles and square show data for samples of estimated phylogenetic trees from the literature: solid triangles, Heard (1992); open triangles, Mooers (1995); square, Guyer and Slowinski (1991). See Mooers and Heard (in press) for more detailed review of this data. (A) Punctuated model; bottom to top $\sigma_x = 0$, 0 1, 0 2, 0.3, 0.4, 0 8, and 1 2 (B) Gradual model; bottom to top $\sigma_x = 0$, 0.02, 0.05 0.1 0.2, 0.4, and 0 6. Inset shows behaviour of I with increasing σ_x for three vertical slices across the main plot: trees of 6, 25 and 50 species
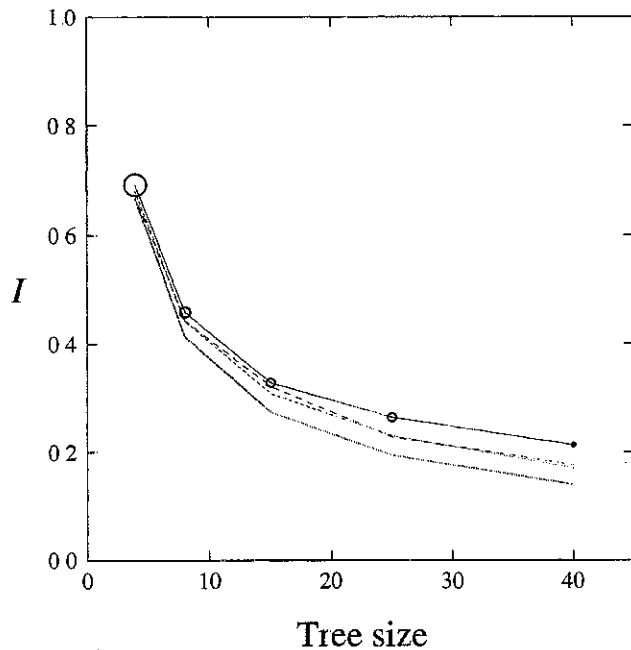
FIG. 4. Imbalance under three models for trait evolution (Table 1A). For all curves, evolution is punctuated and $\sigma_s = 0$ For the linear-Brownian models (bounded below, long dashes; bounded above and below, short dashes), $\sigma_x = 4.75$ For the log-Brownian model (solid line), $\sigma_x = 0.2$; this value gives comparable changes in x for a one-standard-deviation change at the first iteration. The lower dashed line is the Markov expectation Hollow circles cover 95% confidence intervals around simulation results

similarly in describing imbalance (see also Kirkpatrick and Slatkin 1993), and so I report only results for I, which is computationally the simplest of the three.

I calculated means and standard errors for I, from the 2000 simulations, for each evolutionary scenario and separately for each tree size. Tree size must be considered explicitly because, for combinatorial reasons, imbalance declines for larger trees, both for real trees and for the theoretical models considered here (Heard 1992 and results below) I examined trends in imbalance (plotted against tree size) among evolutionary scenarios and with increasing rate variation (increasing σ_x and σ_s). I did not conduct formal statistical analyses, because differences were so clear: in all plots (Figs. 3–5), approximate 95% confidence intervals (mean ± 2 SE) would be hidden by the hollow circles shown on the top curves These confidence intervals narrow with increasing tree size, as does the variance in the equal-rates Markov distribution of I (Rogers 1994). I also plotted (Fig 3) mean imbalance indices for several samples of estimated (literature) trees compiled by Guyer and Slowinski (1991), Heard (1992), and Mooers (1995)

RESULTS AND DISCUSSION

Under most models of speciation-rate variation (Table 1), imbalance increases with increasing rate variation. The only exception is speciation rate noise under the continuous model, which does not affect tree balance
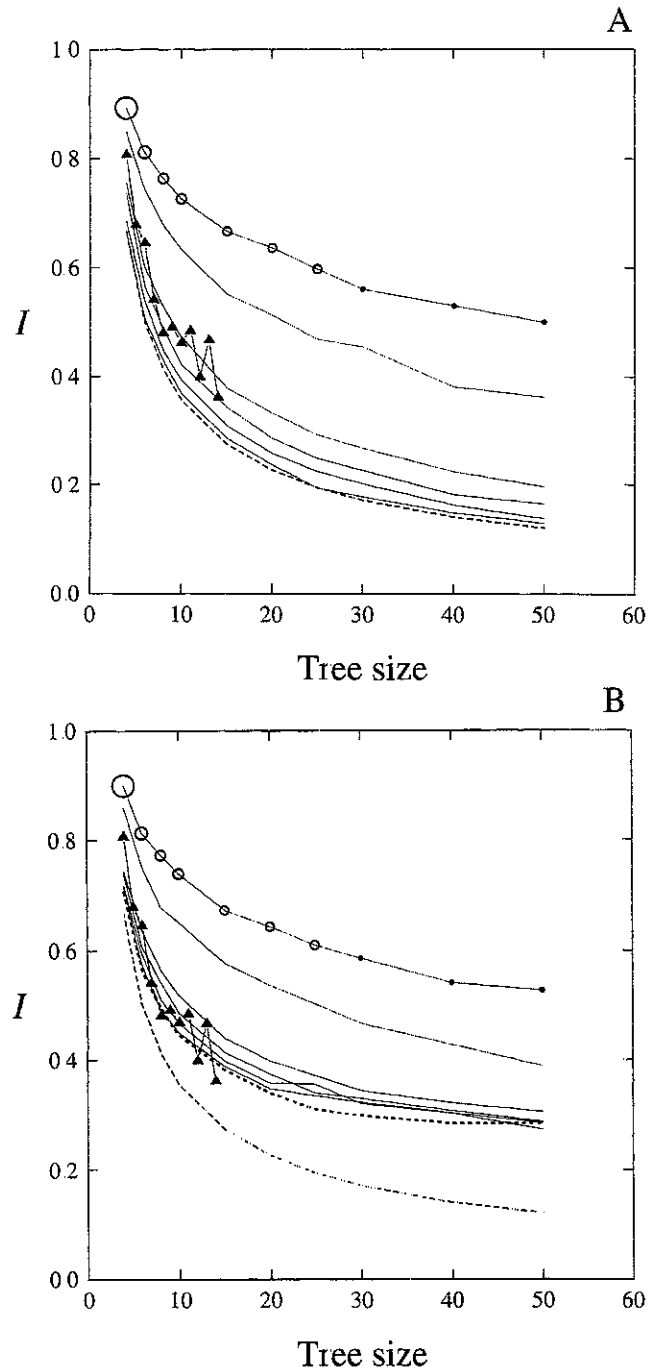

FIG 5. Imbalance with intermittent errors in speciation rates (Table 1C). For all curves, evolution is punctuated and trait evolution is log-Brownian. The lower dashed line is the Markov expectation Hollow circles cover 95% confidence intervals around simulation results. Triangles show data for Heard's (1992) samples of estimated trees. (A) Errors alone: $\sigma_x = 0$; bottom to top $\sigma_s = 0.1$, 0.2, 0.3, 0.4, 0.8, and 1.2 (B) Errors and trait evolution: $\sigma_x = 0.3$ (except Markov curve); bottom to top $\sigma_s = 0.1, 0.2, 0.3$ 0.4, 0.8, and 1.2

Speciation Rate Entirely Determined by x ($\sigma_s = 0$).—When speciation-rate variation is entirely due to the evolution of the underlying quantitative trait, under all models of change imbalance increases with the rate (σ_x) of stochastic change in the trait value.

That imbalance should increase when speciation rates depend on an evolving trait is not surprising This kind of heritable rate variation has been invoked to account for spectacular examples of imbalanced phylogeny such as the dominance of passerines among birds (small body size hypothesized to allow high speciation rates; Kochmer and Wagner 1988) Such variation is also held to drive species sorting under the effect hypothesis (Vrba 1980, 1984): it is predicted to generate trends in trait values through evolutionary time, because those species with extreme trait values and therefore the highest speciation rates come to dominate the clade Such a phenomenon did occur in my simulations (unpubl data; see also McShea 1994)

The effect of evolutionary rate on imbalance depends on the mode of evolution For punctuated evolution, the increase is linear, up to an eventual fall-off imposed by the fact that *I* cannot exceed one (Fig 3A; Rogers [1996] has also simulated this case, with identical results) In contrast, for gradual evolution the increase in *I* is not linear (Fig. 3B, see inset): as σ_x increases, imbalance increases quickly at first but comes to an aysmptote (well short of the theoretical limit of one) when σ_x is very large I discuss this behavior further below Short of the asymptote, much smaller σ_x is required to produce a given degree of imbalance under the gradual model This is essentially because (compared to punctuation) trait values change much more often and therefore differences accumulate faster

The difference between punctuated and gradual models does not depend on other elements of the evolutionary scenario (i.e , Table 1 A, C) In what follows I show only the punctuational results. The linear-Brownian models of trait value change differ little from the log-Brownian (Fig. 4) except that large trees accumulate less imbalance under the linear-Brownian model than under the log-Brownian. Log-Brownian trait evolution has a more strongly imbalancing effect than does linear-Brownian because the compounded nature of change in the log-Brownian model allows wider variation in *x* This effect is most noticeable for large trees, where the compounding occurs over more time.

Adding Other Variation to Speciation Rate.—Continuous noise in speciation rates (Table 1C) has no effect on imbalance, either alone or when applied alongside trait evolution (data not shown) Intermittent noise, in contrast, does contribute to imbalance (Fig 5), although less strongly than comparable variation imposed directly on trait values (Figs 3, 4). This is true whether the intermittent noise acts alone (Fig 5A) or in concert with trait evolution (Fig 5B)

The "noise" component of speciation rate represents variation unrelated to the evolving trait values, and therefore in a sense not "heritable " That continuous- and intermittent-noise models behave differently is potentially very important, not least because previous discussions of such nonheritable variation (e g , Kirkpatrick and Slatkin, 1993, p 1179) have not clearly distinguished the two possibilities. Why does the intermittent-noise model lead to imbalance while the contin-

uous-noise model does not? Intermittent noise is "nonheritable" in the sense that the noise component of speciation rate is discarded and randomly redrawn each time the rate is recalculated. However, it is retained in a lineage in the absence of a speciation event. This generates imbalance even in the absence of trait evolution, because lineages which (by chance) are assigned low speciation rates tend to retain them: only by speciating could they regain a high speciation rate, but only with a high speciation rate are they likely to speciate This catch-22 keeps these lineages depauperate, and the resulting tree is imbalanced Continuous noise, on the other hand, allows no such semipermanent exclusion of lineages, and does not generate imbalance. Whether continuous- or intermittent-noise influences on speciation rates are more important in real clades is unknown, as the evolutionary ecology of speciation rates has not been well studied (Heard and Hauser 1995).

Saturation of Imbalance —For the gradual model, but not for punctuated equilibria, imbalance saturates with high rates of evolution This behavior has not previously been reported Eventual saturation is imposed by the boundedness of the imbalance index *I*, but the observed saturation is well short of this theoretical limit This observation is not in conflict with the existence of individual phylogenetic trees that are apparently beyond the saturation point, because for single trees balance is stochastic and a full range of *I* is possible

Why do the two models behave so differently? Under the punctuated model, a species acquiring a small trait value (and therefore a low speciation rates) is stuck in a situation rather like the one described for intermittent errors Such a species can acquire a higher speciation rate only with a change in trait value, but such a change can only happen if it speciates, which is unlikely precisely because of the small trait value Under the gradual model trait evolution and speciation are decoupled, and no species gets similarly stuck

The difference in behavior between the gradual and punctuated models may allow us to use phylogenetic trees to distinguish between these two major modes of macroevolution Samples of trees with *I* significantly above the asymptotes for gradualism (Fig 3B) could only have been produced under a punctuated mode of evolution (unfortunately, values of *I* below the asymptotes are uninformative) However, for two reasons we cannot yet make such a test First, more detailed modeling will be required to identify the locations of the asymptotes under a variety of evolutionary models. Second, existing compilations are of small trees which fall under the asymptotes for their sizes Larger trees might provide more information, but so far, too few well-resolved, large trees are available.

Imbalance of Estimated Trees —Imbalance indices for literature trees (Fig 3) fall among the simulated values Sample sizes for the literature trees are variable: 120 for the solid square (Guyer and Slowinski 1991), from 7 to 35 for the solid triangles (Heard 1992), and from 4 to 8 for the open triangles (Mooers 1995) Confidence intervals (not shown) generally span the plotted curves shown here, but taken as a single sample, literature trees are strongly and significantly more imbalanced than the Markov expectation (Guyer and Slowinski 1991; Heard 1992; Mooers 1995; Mooers and

Heard in press) Can speciation-rate variation account for this, as I suggested earlier (Heard 1992)?

Precise comparisons are difficult to draw, but the literature numbers correspond to quite large values of σ_x and/or σ_s (either or both could contribute to the imbalance of a tree) For instance, Heard's (1992) trees (Figs. 3, 5; solid triangles) correspond roughly to values of $\sigma_x = 0.3$ under punctuated evolution or $\sigma_x = 0.02$ under gradual evolution, if all rate variation is driven by changes in x These are very large parameter values: with punctuated log-Brownian trait evolution, $\sigma_x = 0.3$ means that about a third of speciation events have x changing by more than a factor of two. Under other evolutionary models, similarly large changes in trait values, or strong noise components of speciation rates, would be required to reproduce the literature values Kirkpatrick and Slatkin (1993) reached a similar conclusion for a related evolutionary model It is, of course, possible that more modest changes in multiple traits, acting in concert on speciation rates, could account for observed levels of imbalance However, this would require that these multiple traits act on speciation rates in the same direction, and perhaps this is unlikely More sophisticated models for speciation rates would be illuminating

While we cannot rule out such strikingly large rate variation, these results at least serve to stress the importance of looking for other factors affecting the topology of estimated trees (Mooers and Heard in press). Suggestions that the use of parsimony significantly biases estimated trees towards imbalance (e.g., Colless 1982, 1995; Kirkpatrick and Slatkin 1993; Mooers et al. 1995) have been questioned (Heard 1992; Heard and Mooers 1996), but other methodological details of tree estimation require further attention For instance, nonrandom omission of taxa when estimating a tree can contribute to imbalance (Mooers 1995)

Other authors have taken a somewhat different approach to the comparison of tree balance between theoretical models and real data, preferring to treat a single phylogeny in detail and estimate speciation rates for lineages within that one phylogeny See Purvis et al (1995) for an example and Mooers and Heard (in press) for a review

CONCLUSIONS

Previous discussions of the imbalance effects of variable speciation and extinction rates have been qualitative and often vague about the kinds of variation in question (e g , Guyer and Slowinski 1991; Heard 1992; Kirkpatrick and Slatkin 1993). The simulations I report here clarify the effects of different evolutionary models and establish some quantitative relationships between rate variation and imbalance They also reveal a previously unsuspected saturation behavior that may allow us to distinguish between gradualism and punctuated equilibria in the evolutionary history of real clades

As suspected, variation in speciation and extinction rates among lineages within a clade does tend to produce imbalanced phylogenetic trees, reminiscent of those seen in the systematic literature Even some nominally nonheritable variation (intermittent-noise model) produces imbalance However, not all variation produces imbalance, and the strength of the imbalance effect depends on the evolutionary model

Despite this dependence on model details, it is clear that estimated trees from the literature correspond to very high, perhaps even implausibly high, levels of rate variation Further exploration of tree topology will be valuable, because imbalance is a fundamental attribute of phylogenies and levels of imbalance are critical to macroevolutionary hypotheses about species sorting and selection, vicariance and its role in diversification, and key innovations (Mooers and Heard in press).

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