



Phylogenetic extinction rates and comparative methodology

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Species are not independent points for comparative analyses because closely related species share more evolutionary history and are therefore more similar to each other than distantly related species. The extent to which independent-contrast analysis reduces type I and type II statistical error in comparison with cross-species analysis depends on the relative branch lengths in the phylogenetic tree: as deeper branches get relatively long, cross-species analyses have more statistical type I and type II error. Phylogenetic trees reconstructed from extant species, under the assumptions of a branching process with speciation (branching) and extinction rates remaining constant through time, will have relatively longer deep branches as the extinction rate increases relative to the speciation rate. We compare the statistical performance of cross-species and independent-contrast analyses with varying relative extinction rates, and conclude that cross-species comparisons have unacceptable statistical performance, particularly when extinction rates are relatively high.

Keywords: evolution; phylogeny; extinction; comparative analysis; independent contrasts

1. INTRODUCTION

If two characters have evolved according to a model of Brownian motion through evolutionary time, then cross-species correlations do not provide reliable statistical estimates of the evolutionary covariance of the characters (Felsenstein 1985). For example, if the characters evolved with no covariance, the null hypothesis of zero covariance will be subject to inflated type I error, so that apparent significant covariance will be detected more often than expected (Martins & Garland 1991). The reason for the apparent covariance is that all species other than those separated since the first speciation event will have shared parts of their evolutionary history in common, so the characters will not actually have evolved independently of each other. This inflated type I error will be greater when many species share a higher proportion of their evolutionary history in common, such as when deeper branches in the phylogeny are relatively longer. Felsenstein's (1985) method of independent contrasts was designed to correct for species non-independence by defining statistically independent comparisons for analysis.

Independent-contrast analysis has become a fairly standard procedure when estimating the evolutionary covariance between and among morphological, behavioural and life-history characters. But it is the nature of science that once a position becomes orthodox it should be subject to criticism. Despite simulation studies that demonstrate considerable type I error (Martins & Garland 1991), several recent papers have argued that cross-species comparisons make reasonable approximations and might often be used in place of independent-contrast analyses (Westoby *et al.* 1995*a,b*; Martin 1996; Ricklefs & Starck 1996; Price 1997). The claim may seem

particularly appealing because cross-species analyses do not require that a phylogeny be known. In fact, it can be shown that cross-species comparisons are valid when the phylogeny is a star, that is when all pairs of species share the same, most-recent common ancestor (Harvey & Pagel 1991). Unfortunately, those advocating the use of cross-species comparisons seem to be making the implicit assumption that a star phylogeny is the best available representation of the unknown phylogeny; this seems unwise. The primary purpose of this paper is to point out that real phylogenies used in comparative biology are likely to possess a structure such that many species share more evolutionary history than has been commonly assumed, and consequently that cross-species analyses are prone to even higher type I error than has been previously estimated.

The most common specified phylogeny simulation procedure is a Yule process where all lineages in a phylogeny have the same probability of splitting (speciating) at any point in time (although many authors base their simulations of character evolution on reconstructed phylogenies for specified clades). The Yule process is a pure birth process, with an implicit extinction rate of zero. In fact, extinction is common in the natural world and when phylogenies reconstructed from a full sample of extant species are available, it is possible to estimate speciation and extinction rates (λ and μ , respectively) in the absence of a fossil record, so long as each parameter has remained constant in time during the generation of the phylogenetic tree (Nee *et al.* 1994*a,b*). As μ increases relative to λ , deeper branches become relatively longer (see figure 1) because sister lineages of those surviving are more likely to have gone extinct, and nodes which would have been present on a full phylogeny that contains records of extinction will be missing from the

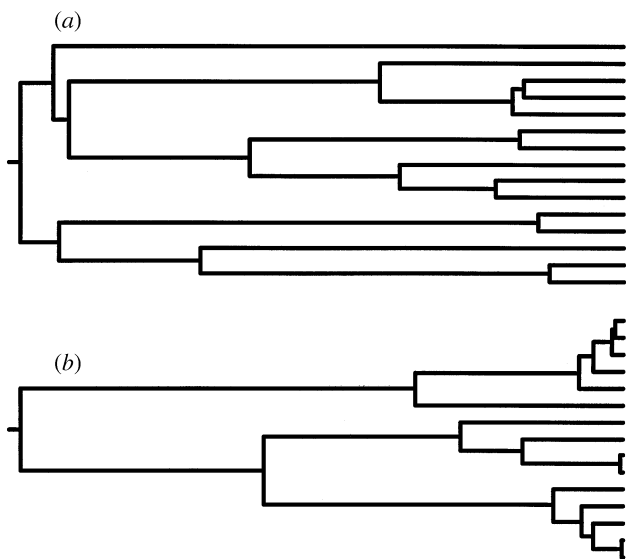


Figure 1. Two representative trees with 15 extant species simulated under speciation (λ) and extinction (μ) processes. (a) $\mu=0$; (b) $\mu=0.95\lambda$. Note that, compared with (b), nodes in (a) tend to occur further back in time relative to the root of the tree, so that shared evolutionary history is reduced.

reconstructed phylogeny which does not. The consequence is that, in a phylogeny reconstructed from extant species, the rate of accumulation of new lineages early in time is $\lambda - \mu$, whereas the rate increases towards λ near the present (Harvey *et al.* 1994). The increase towards the present is a consequence of the fact that recently evolved branches have had less time to go extinct than have deeper branches.

With trees generated under a constant-rates speciation-extinction process, type I error in cross-species analyses might be expected to increase with μ relative to λ , because deeper branches will be relatively longer and there will be more shared evolutionary history in the tree as a whole. Indeed, as we shall show, if $\mu=0.95\lambda$ in phylogenies constructed from 30 species, when the true evolutionary covariance is zero, type I error (with reference to a nominal p -value when $\alpha=0.05$) from cross-species analysis is about 44%. This means that, if there had been no evolutionary covariance between two characters, on almost half of occasions a cross-species comparison would show a significant correlation between them at $p < 0.05$. With larger trees, type I error is even higher, so that for a phylogeny with 150 species, the equivalent type I error is 68%. In addition to examining type I error, we also report power analyses ($1 - \text{type II error}$). It is important to emphasize that, although stochastic processes are involved in tree generation and character evolution, the tree used for comparative analysis is the actual tree along which characters have evolved. We are therefore analysing a process in which the phylogenetic tree has been 'reconstructed' without error.

2. METHODS

Phylogenies containing 15 and 30 extant species were evolved under a constant-rates birth-death process with $\lambda=0.2$ and $\mu=0, 0.1, 0.15$ and 0.19 using the computer application BI-DE

(Rambaut *et al.* 1996). One-thousand phylogenies were produced for each combination of parameter values, making a total of 8000 trees. Two characters were evolved from the roots of the trees to the tips according to a model of Brownian motion with no evolutionary covariance, and with correlations of 0.25, 0.5 and 0.75. Cross-species correlation coefficients were then calculated for each tree, as were phylogenetically independent contrasts that were standardized by branch length. The proportion of correlation coefficients significantly different from zero at the 0.05 level of probability are plotted for each set of parameter values in table 1*a,b*. When the value of r is zero, table 1*a,b* provides estimates of the type I error (here and throughout this paper, statistical error is calculated with reference to the nominal p -value when $\alpha=0.05$). When the value of r is not zero, the table gives estimates of the proportion of tests that reject the incorrect null hypothesis of zero covariance when the simulations are performed under evolutionary correlations of 0.25, 0.5 and 0.75. The 1000 simulated distributions with $r=0$ for each tree size and value of μ were used to determine whether the null hypothesis that $r=0$ was rejected by the data (Martins & Garland 1991). The measure of power is $1 - \text{type II error}$ and, of course, the power is likely to be greater when the hypothesis to be rejected (zero covariance) has a covariance that differs most from the model under which the data were simulated (correlation coefficient of 0.75).

3. RESULTS

Type I error for independent contrasts under the null hypothesis of no character covariance is always about 5%, which is as expected because the method was developed for the model used in the simulations. Type I errors for the cross-species comparisons are higher than for contrast analyses and also higher for (i) larger phylogenies and (ii) when μ is increased relative to λ . For example, when μ is zero, type I error for a phylogeny of 15 species is 24%, but for a phylogeny of 30 species it rises to 29%. However, when μ is 0.95λ , type I error for a 15-species phylogeny is 32% and for a 30-species phylogeny it is 44%. These are extremely high type I errors, and clearly cross-species comparisons do not provide an acceptable procedure for estimating evolutionary covariance with statistical confidence limits, particularly when the phylogeny has been produced under conditions where the per-lineage extinction rates have been appreciable. Note that, for the cross-species comparisons, the increase in type I error as μ increases from 0 to 0.95λ is appreciably greater for the larger tree (15%) than the smaller one (8%). Trees of 30 species are not unusual in modern comparative analyses, and larger trees with even higher type I errors for cross-species comparisons can be expected to become more common as the molecular phylogenetic database enlarges.

The power of a test depends, of course, on the alternative hypothesis under consideration (H1). Three patterns in the power analyses reported here are not surprising. First, for each column in table 1*a,b*, the estimated power increases with $r=0.25$ to 0.5 to 0.75; that is because the null hypothesis to be rejected ($r=0$) differs increasingly from the one under which the data were simulated. Second, the power for any particular cell is greater when the phylogeny is larger; that is because more data are available to compare with the null

Table 1. *Estimates of statistical type I error and power*

(Each cell gives the proportion of 1000 computer simulation runs that differed significantly from the null hypothesis at $p < 0.05$ for trees with (a) 15 tips and (b) 30 tips. r is the evolutionary covariance, λ is the speciation rate, and μ the extinction rate used in the simulation. The rows for $r=0$ give the proportion of times the correct null hypothesis of zero evolutionary covariance is rejected (type I error). When r is greater than zero, the simulated covariance is given by the stated r and the null hypothesis is that $r=0$; the simulated distribution for that tree size, with the appropriate λ and μ and $r=0$, is used to determine whether the null hypothesis is rejected at $p < 0.05$ (1 - type II error; a measure of the power of the test). Note that comparisons between tabulated values for $r=0$ and $r > 0$ are not meaningful because the former is a measure of type I error and the latter of statistical power.)

(a)

r	μ/λ	species				contrasts			
		0	0.5	0.75	0.95	0	0.5	0.75	0.95
0		0.24	0.30	0.30	0.32	0.07	0.04	0.05	0.05
0.25		0.07	0.10	0.08	0.07	0.12	0.15	0.15	0.15
0.5		0.20	0.25	0.18	0.17	0.43	0.50	0.49	0.49
0.75		0.55	0.58	0.49	0.42	0.92	0.94	0.93	0.93

(b)

r	μ/λ	species				contrasts			
		0	0.5	0.75	0.95	0	0.5	0.75	0.95
0		0.29	0.37	0.41	0.44	0.06	0.05	0.05	0.05
0.25		0.11	0.11	0.08	0.11	0.22	0.24	0.26	0.28
0.5		0.35	0.29	0.21	0.26	0.78	0.83	0.81	0.85
0.75		0.81	0.68	0.58	0.60	1.00	1.00	1.00	1.00

hypothesis. Third, for any combination of parameter value (μ and r), tests based on cross-species comparisons are appreciably less powerful than those based on contrast analyses. The first and third of these findings accord with Martins & Garland (1991).

However, the primary purpose of this paper is to determine the extent to which bringing extinction into phylogeny generation alters the statistical properties of comparative tests. For type II error or statistical power, the answer is that we can detect no major influences of increasing μ relative to λ : considering values of $r=0.25, 0.5$ and 0.75 , for neither cross-species nor contrast analyses is there a consistent change in power as we move from left to right along any row of table 1a,b.

Martins & Garland (1991) also considered tree balance as a potential factor influencing the statistical outcome of cross-species versus contrast analyses. They found that for cross-species analyses, extremely balanced phylogenies had markedly higher type I errors than extremely unbalanced or comb-like phylogenies. This finding is not unexpected because the amount of common evolutionary history tends to be least for comb-like phylogenies. How does tree balance influence the phylogenies considered in this paper? Our trees have topologies and branch lengths determined by the vagaries of the speciation and extinction processes inherent in the Markov processes underlying our simulation procedures. There are many measures of tree balance, some of which are summarized by Kirkpatrick & Slatkin (1993). We have calculated all of their reported measures of balance for all of our simulated trees and can find no significant relationship

between tree balance and cross-species correlation coefficient for any measures of relative extinction rate under either size of tree when characters are evolved with no covariance (using the simulations given in the first rows of table 1a,b).

As a cruder method for illustrating the lack of association between tree balance and type I error, we calculated Colless's (1982) index for all the trees, and ranked the 1000 trees generated under each set of parameter values from least to most unbalanced. Then, after evolving two characters independently (with no covariance) from root to tips down the trees, we divided the trees into two classes: those for which cross-species analyses rejected the null hypothesis of character independence (at $p < 0.05$) and those for which the null hypothesis was not rejected. We could find no association between tree balance and deviation from null expectation for trees with either 15 or 30 tips under any relative extinction rate (data for $\mu=0$ and $\mu=0.95\lambda$ are summarized in table 2).

4. DISCUSSION

Both simulation studies and logical inference have led several authors to point out that when more-ancient branches in a phylogeny are longer than more-recent branches, cross-species comparisons are likely to have larger type I errors than analyses of phylogenetically independent contrasts (Martins & Garland 1991; Price 1997). This is true even when the latter are estimated under an assumed null model of Brownian motion, while

Table 2. *The lack of association between tree balance and type I error*

(One thousand computer-simulated trees were generated for each of four conditions: trees with (a) 15 tips and (b) 30 tips, and with $\mu=0$ and $\mu=0.95\lambda$ for both sized trees. For each set of 1000 trees, two characters were evolved independently (i.e. with no covariance) according to a model of Brownian motion from root to tips. Colless's balance index was calculated for each tree. Each set of 1000 trees was divided into the 500 most unbalanced and the 500 most balanced. Within each category of 500, the number of trees for which the null hypothesis of no character covariance was rejected at significantly less than 0.05 and accepted at significantly greater than 0.05 is also recorded in the table. Under each set of conditions, a chi-squared test for independence between tree balance and deviation from the null hypothesis was not rejected at $p < 0.10$.)

(a)

	$\mu=0$		$\mu=0.95\lambda$	
	probability <0.05	>0.05	<0.05	>0.05
>0.05				
unbalanced	115	385	172	328
balanced	122	378	152	348
	$\chi^2=0.27, p=0.60$		$\chi^2=1.83, p=0.18$	

(b)

probability	$\mu=0$		$\mu=0.95\lambda$	
	<0.05	>0.05	<0.05	>0.05
unbalanced	153	347	225	275
balanced	141	359	218	282
	$\chi^2=0.69, p=0.40$		$\chi^2=0.20, p=0.66$	

the true simulated model differs in various ways from Brownian motion (Martins & Garland 1991). We have argued here that relatively longer deeper branches and higher type I errors occur as lineage-extinction rates are increased relative to lineage-splitting rates during the generation of a phylogeny. Our simulations, performed under a model of Brownian motion, demonstrate that type I errors for cross-species analyses increase both with relative extinction rates and with the size of final phylogenies generated under a constant-rates speciation-extinction process: for phylogenies of 15 contemporary species with an extinction rate of zero, the type I error is 24%, but this increases to 44% for 30 species with an extinction rate of 0.95 times the speciation rate. Comparative studies increasingly incorporate data from more than 30 species, together with a reasonably resolved tree. This led us to simulate a larger tree with 150 tips: when $\mu=0.95\lambda$, the type I error had increased to 68% with reference to a nominal p -value when $\alpha=0.05$, and it was 58% for $\alpha=0.01$. Type I errors for contrast analyses stay at about the expected 5%, with both increased extinction rate and larger phylogenies.

The probability of accepting an incorrect null hypothesis, the type II error, is higher for cross-species than for contrast analyses, confirming Martins & Garland's (1991) conclusions. Type II errors are lower for larger phylogenies. It follows that the statistical power is increased for contrast analyses and larger phylogenies.

Our simulations revealed no detectable relationship between type II error and relative extinction rate under a constant-rates speciation-extinction model for phylogenies with the same number of contemporary species.

Given the large type I and type II errors reported in table 2, which together demonstrate the poor statistical performance of cross-species comparisons compared with contrast analyses, we must disagree with Martin (1996) who claims that, with reference to allometric scaling, 'phylogenetic relatedness should not be expected to have much effect on the overall relationship determined'. Indeed, so called 'grade shifts', describing the finding that allometric coefficients often differ between clades whereas allometric exponents do not, means that a single evolutionary change (which in a contrast analysis would be a single aberrant value lying outside the confidence limits of the bivariate plot) can have a pronounced influence on the exponent estimated from cross-species relationships. This is because a single line is fitted through two (or more) logarithmically scaled, bivariate relationships that differ in elevation but not slope; the estimated cross-species correlation can be extremely high while the evolutionary allometric relationship is estimated with considerable error. We shall examine the influence of grade shifts and differential extinction rates on estimates of allometric exponents elsewhere.

Ricklefs & Starck (1996) reported 21 case studies mostly from birds and mammals where logarithmically transformed data have been used to estimate correlation coefficients between a variable and body size for both cross-species and contrast analyses. Price (1997) performed a similar analysis. Not surprisingly, the cross-species and contrast coefficients tend to be similar; after all, they are estimates of the same thing (Felsenstein 1985; Martins & Garland 1991; Pagel 1993). However, in only six cases reported by Ricklefs & Starck (1996) is the contrast correlation higher than the cross-species correlation. Unfortunately, it is not possible to determine the precise statistical significance of this difference between the two methods by a sign test (although it has to be $p < 0.05$, or lower) because, although there are claimed to be 21 studies, there are clearly more points on their graph than that. It is therefore wrong of Ricklefs & Starck to argue that analyses of phylogenetically independent contrasts 'have not exposed pronounced differences or consistent biases in results of regression and correlation analyses of TIP [cross-species] data': their own figure shows a consistent bias for correlation analyses.

Ricklefs & Starck go on to claim that independent-contrast analyses 'need not replace more conventional' cross-species analyses 'especially inasmuch as results of the two approaches for regressions and correlations over entire lineages do not appear to differ significantly'. In many cases the correlation coefficients will not differ significantly from each other (although Ricklefs & Starck do not perform this test), but it may nevertheless be true that a cross-species analysis does not include the correct value in its confidence limits, whereas the independent-contrast analyses do (i.e. the type I error is lower for contrasts than cross-species analysis). To argue, as they do, that contrast analyses lose accuracy when the phylogeny is not well resolved is a red herring: almost any accepted phylogenetic hypothesis will be

more accurate than the implicit cross-species assumption that all species arise from a single common ancestor with no shared ancestry among them since that time (a so-called 'star phylogeny'). Falling back on cross-species analyses when the assumptions of independent contrasts do not hold fully ensures estimating the available statistic that possesses the maximum type I and type II errors! The reason is that there will always be some phylogenetic structure available for analysis and to include that is better than to include none at all. Their claim that the results of independent-contrast analyses 'are relatively insensitive to actual topology or branch lengths' is also misleading, as we have demonstrated in this paper.

Why did Martins & Garland (1991) find a relationship between tree balance and type I error, and we did not? The answer probably lies with the range of tree balances used in the two studies. For trees of the same size (i.e. number of tips), Colless's measure often proves preferable to others because it has an intuitive interpretation, yet is highly correlated with other indices (Heard 1992). Under that measure, Martins & Garland compared trees having a balance of 1.0 (totally unbalanced, or pectinate) with those having a balance near 0.0 (totally balanced; Martins & Garland could not achieve 0.0 for their trees of size 15, because with an odd number of tips, exactly one-half of the tips of such trees cannot lie either side of the root). For our simulation studies, the trees were randomly generated with each branch being equally likely to split, and with a lower probability to go extinct, at any point in time. As with Kirkpatrick & Slatkin's (1993) trees with 15 tips, which were also generated according to a random speciation process, our mode value for Colless's index is strongly peaked around values of 0.2 to 0.3 (see figure 2a). Although the distribution is skewed to the right, only three trees have a value above 0.6. With such a small range of balance, we did not pick up the effect detected by Martins & Garland. The situation is worse for trees with 30 tips, as expected (Heard 1992; Kirkpatrick & Slatkin 1993; Rogers 1993; Mooers *et al.* 1995): the variance is lower, as is the mean (see figure 2b). Errors in tree reconstruction will lead, on average, to trees becoming more unbalanced (Mooers *et al.* 1995).

Our simulations assume that extinction rates remain constant through time. When extinction rates vary through time, the results of phylogenetic analyses must be treated with caution. For example, if all extant species were sampled after a recent mass extinction, this would produce a similar phylogenetic outcome to sampling a smaller number of species from a clade in which there had been no mass extinction. As a consequence, for reasons explained below, background speciation rates would be underestimated if we did not know there had been a mass extinction. If both λ and μ had remained constant through time, on a semi-logarithmic lineages-through-times plot, the slope would have been *ca.* $\lambda - \mu$ in the more distant past, but λ in the recent past (Harvey *et al.* 1994). With a recent unrecognized mass extinction, the slope in the recent past will be underestimated, and μ will consequently be estimated as a lower proportion of λ during the periods of background extinction. For example, if λ is really 0.6 but is

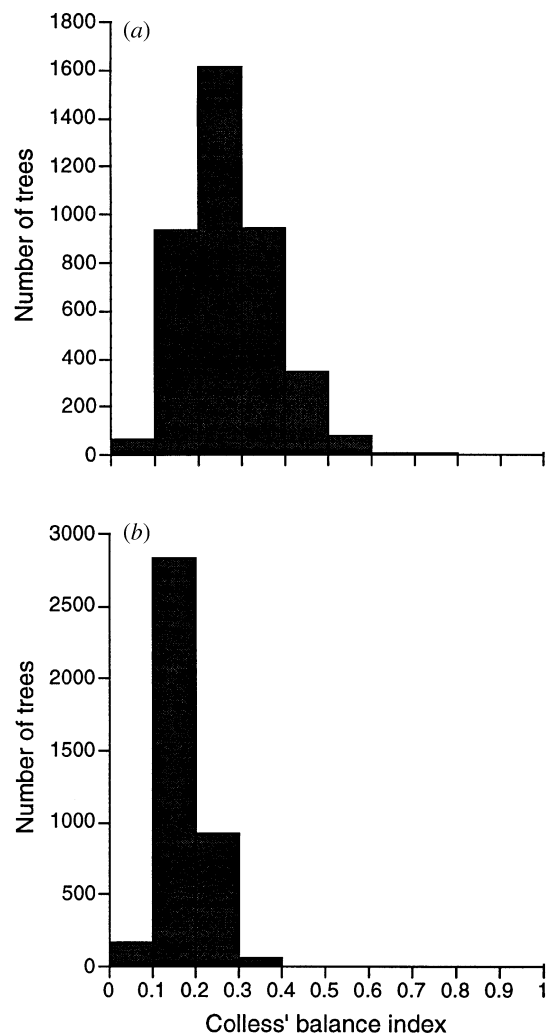


Figure 2. Colless's balance index for (a) 4000 trees with 15 tips, and (b) 4000 trees with 30 tips. In both (a) and (b), trees generated under constant-rates speciation-extinction models, with a per-lineage speciation rate $\lambda=0.2$ and per-lineage extinction rates $\mu=0, 0.5\lambda, 0.75\lambda$ and 0.95λ , have been amalgamated because there was neither an expected nor a realized difference in tree balance with changes in the per-lineage extinction rate. Both the mean and variance of the balance index decreases for trees with more tips; reasonable comparisons can be made only within tree size classes, not between them.

estimated as 0.4, and $\lambda - \mu$ is 0.3, the real μ is 0.3 but would be estimated as 0.1. So, a μ/λ of 0.5 would be estimated as 0.25.

Standardized, phylogenetically independent contrasts were estimated here, as is usual, under a Brownian-motion model of character evolution. What if characters evolve according to some other model of evolution? Díaz-Uriarte & Garland (1996) report the results of an extensive series of computer-simulation studies in which characters were evolved under 15 different models of character evolution. In general, cross-species comparisons yielded high type I errors, whereas independent contrasts calculated under the model of Brownian motion generally performed well, with type I errors never exceeding 10%. One model that is common to a variety of simulation studies is the so-called punctuational model in which

character change occurs in only one daughter lineage and only immediately at the speciation event (i.e. at lineage splitting). A problem here which is often overlooked, or at best mentioned in passing, is that many nodes in a real phylogenetic tree will be missing from a phylogeny that has been reconstructed from contemporary species because lineages that have gone extinct leave no record of ever having existed. Under the punctuational model with lineage extinction, character change may well have occurred along reconstructed branches with missing nodes that would have led to now-extinct lineages.

A particularly innovative and possibly more realistic model of character evolution has been suggested by Price (1997). Here, available niches have dimensions that covary, character covariation is determined by niche occupancy; species invading new niches are those most adapted to them (i.e. lie closest to them in coordinate space), and speciation follows invasion of a new niche. Price's model, which was simulated to compare the results of cross-species and contrast analyses for phylogenies of ten species, has not yet been developed to deal with lineage extinction. We shall report the results of such analyses elsewhere.

It has not been our intention to review the literature on the wide range of extinction rates estimated from different taxa. Instead, our purpose has been to examine a potential source of statistical error in cross-taxonomic analyses so that future studies might incorporate it as a relevant variable. However, to give some idea of the magnitude of possible extinction rates, we note that Nee *et al.* (1994a) provide an estimate of background extinction rate being 0.87 times the speciation rate in the plethodontid salamander phylogeny, which is used by many workers as a case study for comparative analysis methodology! Furthermore, for reasons outlined above, recent mass extinctions and taxon undersampling (which is formally equivalent to a wave of recent extinctions) will lead to underestimates of background extinction rates. Both recent mass extinctions and taxon undersampling are likely to be common but overlooked in empirical studies.

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