Comparative analyses for adaptive radiations

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Biologists generally agree that most morphological variation between closely related species is adaptive. The most common method of comparative analysis to test for co-evolved character variation is based on a Brownian-motion model of character evolution. If we are to test for the evolution of character covariation, and we believe that characters have evolved adaptively to fill niches during an adaptive radiation, then it is appropriate to employ appropriate models for character evolution. We show here that under several models of adaptive character evolution and coevolution during an adaptive radiation, which result in closely related species being more similar to each other than to more distantly related species, cross-species analyses are statistically more appropriate than contrast analyses. If the evolution of some traits fits the Brownian-motion model, while others evolve to fill niches during an adaptive radiation, it might be necessary to identify the number of relevant niche dimensions and the modes of character evolution before deciding on appropriate statistical procedures. Alternatively, maximum-likelihood procedures might be used to determine appropriate transformations of phylogenetic branch lengths that accord with particular models of character evolution.

Keywords: comparative method; evolution; adaptation; ecological niche

1. INTRODUCTION

John Maynard Smith's book *Models in ecology* (Maynard Smith 1974) introduced to many the idea that parameters used in ecological models are subject to evolution by natural selection. The purpose of this paper is also to increase the dialogue between ecology and evolution, but in the reverse direction, by introducing ecological considerations into a class of widely used evolutionary models.

Comparative analyses frequently examine the correlation between traits across taxa, often with the aim of testing whether two particular traits tend to covary. It has become increasingly accepted that species values for traits might not provide statistically independent points for comparative analyses because more closely related species tend to be more similar on almost any trait that we care to examine. Felsenstein (1985) introduced the method of 'independent contrasts', which defined independent units for statistical analysis of traits undergoing evolution according to a Brownian-motion model. If the traits had been evolving independently, under an independent contrast analysis the correlation between contrasts should be zero. Independent contrasts have come to be used almost routinely in comparative analyses, partly because they seem to provide much less inflated statistical error (and often more statistical power) than cross-species comparisons, even when the traits have not been evolving in a strictly Brownian-motion fashion (Martins & Garland 1991; Diaz-Uriarte & Garland 1996, 1998).

There have been several criticisms of independent contrast analyses, and some have suggested that cross-species analyses might often be appropriate (Ricklefs & Starck 1996). However, in the absence of an explicit model of evolution that justifies cross-species comparisons (except the trivial case in which all pairs of species in a sample share the same most recent common ancestor), independent contrast analysis has seemed generally to be justified (Harvey & Rambaut 1998). However, Price (1997) described a non-Brownian-motion model of character evolution during an adaptive radiation in which closely related species do indeed tend to be similar but in which cross-species analyses seemed to perform as well as independent contrasts. As we shall show, cross-species comparisons in fact perform better than independent contrasts under Price's model, and at least as well under other related models that include evolutionary time-lags, extinction, and restrictions on the ability of species to invade niches that are dissimilar from those that they currently occupy. We emphasize that particular models of adaptive character evolution as well as neutral evolution might well produce character state distributions that, when mapped on to phylogenies, accord with the expectations of the Brownian-motion model and should not be subject to cross-species analysis (Felsenstein 1985; Martins & Garland 1991; Diaz-Uriarte & Garland 1996, 1998).

Price's model, which derives from verbal models given elsewhere (Grafen 1989; Harvey & Pagel 1991) captures the essence by which many evolutionary biologists might consider that adaptive radiations have evolved and why characters tend to covary (Harvey & Pagel 1991). In essence, from time to time a physical niche becomes open to occupancy by a species, which invades the niche, evolves morphological, anatomical, life-history and behavioural traits that adapt it to the new environment, and speciates. The biotic and abiotic environments to which species adapt define niches. When there are fewer
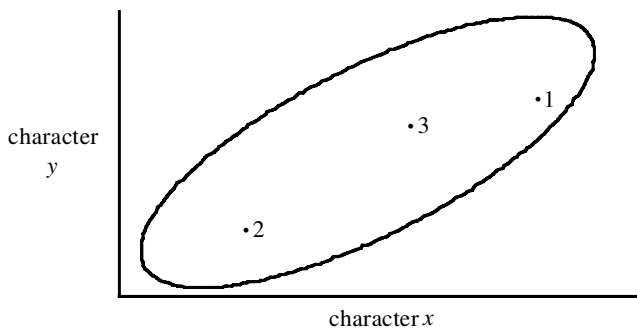
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Figure 1. The basic model used for the simulations described in this paper, and developments of it. The optimum values for characters *x* and *y* are determined by the niches that species occupy, and correlations between characters result from niche structure. Niches appear so that the optimum for characters *x* and *y* are correlated according to a bivariate normal distribution with correlation *r*; the ellipse represents the 95% confidence limits of that distribution. The optimum values of *x* and *y* for three species are shown. The niches appeared sequentially in numerical order. A new niche is invaded by the species with the closest euclidean distance to it in character space. Under that basic model, niches 2 and 3 will be invaded by the species occupying niche 1. That ordering might change as variants to the model are incorporated. With evolutionary lag, the species occupying niche 1 invades niche 2 but it takes a long time, relative to the rate of appearance of new niches, for the optimum character states to evolve. When niche 3 appears, the species occupying niche 2 will invade niche 3 if it is closer in phenotype space to the optimum value for niche 3 than is the occupant species of niche 1. With the maximum-distance niche shift, the species occupying niche 1 might be sufficiently dissimilar from the optimum value for niche 2 that it cannot maintain a viable population there. Niche 2 will then be unoccupied until a species with a phenotype sufficiently close to the optimum for niche 2 can invade it. The species that comes to occupy niche 3 might be that species after it has evolved the requisite phenotype. With extinction, the species occupying niche 1 might become extinct after niche 2 has been invaded but before niche 3 has appeared, so that the species occupying niche 2 invades niche 3.

independent niche dimensions than there are traits, some traits will be correlated with others. Vacant niches are likely to be invaded by species that are already reasonably well adapted to them and are thereby able to produce viable populations that out-compete other invaders. As a consequence, closely related species will tend to be more similar to each other; this is what Harvey & Pagel (1991) termed 'phylogenetic niche conservatism'. Here we develop this model to incorporate biological realism (figure 1) in a series of statistical simulation studies. We find that cross-species comparisons generally perform better than independent contrasts, and often have acceptable statistical properties. This need not be surprising because it is not the model of evolution that Felsenstein used to develop independent contrasts. As it is well established that cross-species analyses and independent contrast analyses often provide different statistical conclusions when analysing real data sets (Harvey & Purvis 1991), the use of independent contrasts or cross-species procedures should be justified.

2. THE BASIC MODEL

Characters covary as a consequence of selection determined by the niches that species occupy: niches that select for particular values of trait *x* also tend to select for correlated values of trait *y*. A new niche that arises is invaded by that extant species whose phenotype is closest to the optimum for the vacant niche. Price (1997) envisages a bivariate normal distribution for *x* and *y*, with specified correlation *r*. If a new niche arises for which the optimum phenotype is too close (less than a specified euclidean distance) to one already occupied, the new niche is deemed not to have arisen because gene exchange ensures that the two populations occupying very similar niches would not speciate. In his reported simulation of the model, which started with a species occupying a randomly placed niche, Price seems to have assumed that new niches arise with equal probability anywhere within the 95% confidence limits of the bivariate normal distribution for character optima determined by niche occupancy, but that no niches could arise outside those limits. Our basic model is a refinement of Price's in that the relative probabilities of the positions of new niche optima appearing in character space are given by the bivariate probability density function specified in the underlying model.

3. DEVELOPMENTS OF THE MODEL

(a) *Procedure*

One of the most problematic aspects for comparative analyses that have not been phylogenetically controlled is that phylogenetic non-independence can lead to statistically significant cross-species correlations between traits that have, in fact, been evolving independently of each other. Accordingly, under a variety of evolutionary models incorporating independent niche dimensions that do not produce an evolutionary correlation between characters *x* and *y*, we have run simulations and tested for significance of the product moment correlation coefficient *r* at the $p < 0.05$ significance level. We ran 1000 simulations for each set of variables, with the expectation that the 'correct' null hypothesis of $r = 0$ should be rejected on 5% of occasions. Using this procedure, we estimated the type I error for a nominal value of $\alpha = 0.05$ by using cross-species, standardized contrast analyses with branch lengths proportional to time (time-scaled contrasts), and standardized contrast analyses with all branches in the phylogeny being of equal length (contrasts with equal branch lengths). Under a Brownian-motion model of character evolution in which phenotypic variance between lineages tends to increase with the time because the lineages last shared a common ancestor, time-scaled contrast analysis, which takes branch lengths into account, is the appropriate procedure. Under Price's basic model, in which all evolutionary change takes place at speciation, branch length does not in itself influence the amount of evolutionary change expected and therefore contrast analyses that assume equal branch lengths might be more appropriate. However, as niche space fills, successive speciation events tend to result in smaller changes in character state, so the assumption of equal branch length would not be expected to be wholly

appropriate. Furthermore, character change occurs on only one branch leading from each speciation.

Standardization of a contrast requires making its mean independent of its standard deviation. Garland *et al.* (1992), and previous papers cited therein, suggest that one useful test for the adequacy of standardization is to check that there is no correlation between the absolute value of a standardized contrast and its standard deviation (the square root of the sum of its branch lengths). We have used that diagnostic test to examine whether, in situations when type I error rates are high, there is a significant correlation between standardized contrasts and their estimated standard deviations. If the diagnostic is effective, when type I errors are high we should expect the proportion of correlations significant at the $p < 0.05$ level to be well above 1 in 20. In such circumstances we should either reject the contrast method as being inappropriate for analysing the data, or find a way of rescaling the contrasts so that standard deviations are independent of means.

Type I error informs us of the probability of rejecting a correct null hypothesis, whereas type II error or power analyses inform us of the probabilities, respectively, of accepting or rejecting an incorrect null hypothesis. To test the power of cross-species analyses, time-scaled contrast analyses and contrast analyses with equal branch lengths, for each set of conditions we ran 1000 simulations with $r = 0.75$. Then, using the simulated distribution for $r = 0$, we determined the frequency of occasions in which the incorrect null hypothesis of $r = 0$ failed to be rejected at the $p < 0.05$ significance level when r was in fact 0.75.

(b) *The refined basic model*

We considered niches that arose sequentially in time according to a temporal Poisson process with parameter 1.0. Each niche determined optimal values for two traits x and y, normally distributed in niche space with means of 0.0 and variances of 1.0. When a new niche arose, it was given x- and y-coordinates sampled from the probability density function provided by the bivariate normal distribution with the appropriate value of r. Any niche that appeared within a distance of 0.01 from an extant niche was ignored. The first niche to arise was considered occupied and subsequent niches were invaded by the extant species that had the shortest euclidean distance from it in phenotype space. Although the second niche to appear would always be invaded by the species occupying the first niche, close relatives would tend to be phenotypically similar as the simulation progressed.

Despite the similarity of close relatives, under this model, cross-species analyses would be expected to provide acceptable type I errors for trees with varying numbers of tips (extant species); this was found to be so (figure 2*a*). The reason is that species will be placed in phenotype space according to the probability density function underlying the null hypothesis to be tested, with the exception that the minimum-distance criterion means that results in species become slightly overdispersed. For each successful independent draw from the bivariate normal distribution, at the end of the simulation there will be just one tip with those trait values. As far as our estimate of r is concerned, phylogenetic relationships provide no additional relevant information. Nevertheless,

because unoccupied niches are invaded by species occupying the closest niche in euclidean space, close relatives tend to be similar for both x and y variables.

We provide no analytical justification for performing contrast analyses on simulated output from the basic model, but do so because such analyses have become almost routine. When a new niche is occupied, the close relative speciating into it retains its ancestral state in the niche from which it came. This is not a gradual model of evolution, and branch lengths (assuming that they are in some way representative of time) of the resulting phylogenetic tree provide no information about character change. As a consequence, we performed both contrast analyses, which assume that all branch lengths are equal, and time-scaled contrasts, which do not. As is evident from figure 2*a*, type I error is increased for time-scaled contrasts, doubling for smaller trees and almost quadrupling for larger ones. However, contrasts assuming equal branch lengths give reasonable type I errors for trees containing between ten and 20 species, but the error increases rapidly until it is almost quadrupled with trees containing 100 species; this is perhaps unsurprising because the niche-filling effect resulting in smaller character changes towards the present (mentioned in §1) would probably increase type I errors.

The results of power analyses for $r = 0.75$ (as described in §3(a)) are given in figure 2*b*. Again, cross-species comparisons performed well, with even small trees of 15 species rejecting the incorrect null hypothesis of $r = 0$ on 90% or more of occasions. However, both time-scaled contrast analyses and contrast analyses with equal branch lengths performed markedly less well, particularly for small trees.

For the simulations reported in figure 2*a*, we performed a diagnostic test (Garland *et al.* 1992) seeking a correlation between the value of contrasts and their standard deviations. The test was effective, finding significant correlations between the values of the contrasts and their standard deviations for virtually all of the simulations (table 1).

(c) *Evolutionary lag*

A species invading a new niche will be adapted to the niche from which it came. For example, a seed-eating finch, with a small beak adapted to feeding on small seeds, invading a habitat with large seeds will evolve a large beak to deal with larger food items. We wish to investigate the effect of 'evolutionary lag' so that phenotypes will not immediately evolve to their new optima. When a new niche appears, the species that is currently closest to it in character space will speciate and one of its descendant lineages will occupy that niche. Once it has occupied that niche, it will adapt to the optimum trait values for that niche. Thus, the species will travel across trait space towards its niche's optimum.

A convenient algorithm for incorporating evolutionary lag is to scale trait size change with time. Recall that the expected time between the appearance of successive new species is 1.0 time-unit. The proportion of the euclidean distance moved per unit time between a species' current position in trait space and the optimum position determined by its niche is $d = 2^{-l}$, where l is a positive continuous variable defining the evolutionary lag. When $l = 1$, the species moves half of the distance between its current
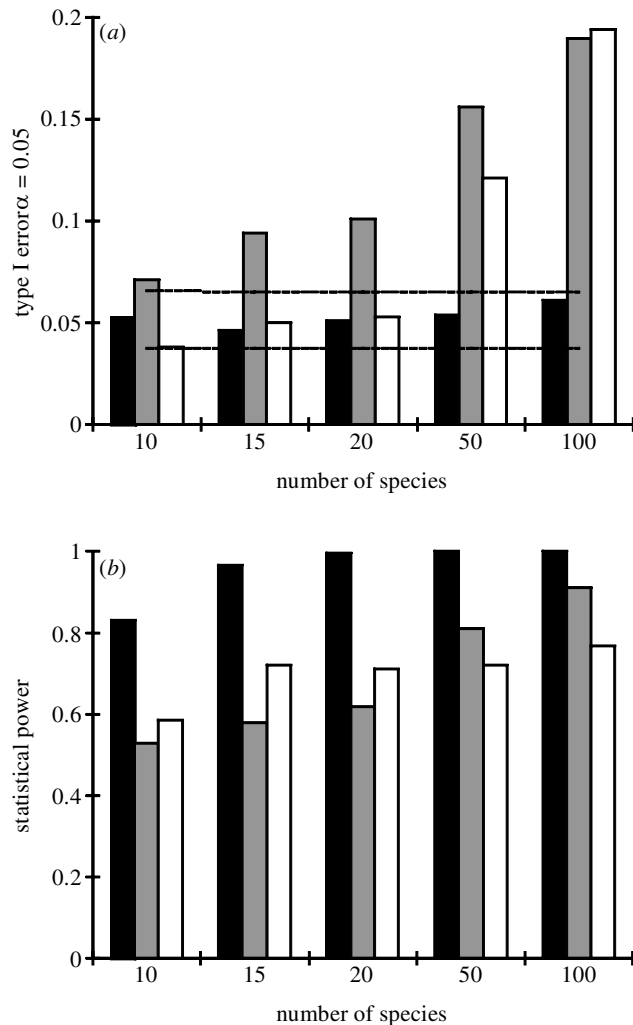
Figure 2. A total of 1000 simulations of phylogenies evolving to each of five tree sizes (10, 15, 20, 50 and 100 tips) under the basic model (no evolutionary time lag, no maximum distance) for each of two conditions of character correlation (0.0 and 0.75). In both (*a*) and (*b*), solid bars refer to cross-species comparisons, grey bars to standardized independent contrasts with branch lengths proportional to time (time-scaled contrasts), and open bars to standardized independent contrasts with equal branch lengths. For the simulations summarized in (*a*), character correlation was zero, and the proportion of trees giving a statistically significant value of the product moment correlation coefficient r at $p < 0.05$, under the null hypothesis that $r = 0$, gives an estimate of the type I statistical error at a nominal value of $\alpha = 0.05$. For the simulations summarized in (*b*), character correlation was 0.75, and the proportion of trees rejecting the null hypothesis that $r = 0$ at $p < 0.05$ provides an estimate of statistical power.

position and its optimum position in euclidean space per unit time. When l is smaller or larger, any species moves relatively longer or shorter distances towards its optimum each time unit.

Considering a phylogeny evolving to a size of n species, under this model with a lag of $l = n$, the second species to appear will have moved about half of the distance required from the niche occupied by the ancestral species towards the optimum for its niche by the time that the final species has appeared. There will therefore be considerable clustering of species in phenotype space when l is large,

Table 1. *Diagnostics test: the proportion of 1000 correlations between values of contrasts and their estimated standard deviations that was significant for simulations reported in figure 2a*

tree size	10	15	20	50	100
time-scaled standardized contrasts	0.996	1.0	1.0	1.0	1.0

and species will not be distributed in trait space according to the bivariate normal distribution. Type I statistical errors for cross-species correlations are satisfactory for small and large trees as long as the evolutionary lag is below about 2 (see figure 3a for trees with 50 tips). Power analyses based on cross-species analyses for rejecting a correlation of 0 when the true correlation is 0.75 are also satisfactory for trees with 20 or more tips, and even for trees with as few as 15 tips when the evolutionary lag is not high (see figure 3b for trees with 50 tips). As with the basic model, cross-species analyses generally have equivalent or lower type I errors than contrast analyses, and contrasts assuming equal branch lengths usually perform better than time-scaled contrasts. Similarly, except when the evolutionary lag is extremely small and trees are very large, contrast analyses lack statistical power when compared with cross-species analyses; time-scaled contrasts perform much less well than contrasts assuming equal branch lengths when evolutionary lag is large.

For the simulations reported in figure 3a, type I statistical errors for contrast analyses are always more than twice the nominal level, and go as high as nine times that level. Again, the diagnostic test proved effective: significant correlations at the $p < 0.05$ level between the values of the contrasts and their standard deviations were found for all 1000 simulations performed for each of the nine time-lags with the use of both time-scaled standardized contrasts and equal-branch-length standardized contrasts.

(d) *Maximum-distance niche shift*

Consider again the example of a finch that is adapted to feeding on small seeds invading a new habitat containing larger seeds, say nuts. It is reasonable to suppose that if a vacant niche opens that is too distant in phenotype space from the nearest that is currently occupied, the new niche will not be invaded because the poorly adapted immigrants could not maintain a viable population there. We introduce here the concept of the maximum niche shift in euclidean space that can be achieved by a species invading a new niche. One characteristic of such a model is that, by chance, a cluster of neighbouring niches can arise, none of which can become occupied until a suitable 'bridging' niche appears between the cluster and an occupied niche; however, once that happens, an immediate cascade of niche filling occurs.

Introducing a maximum distance from which unoccupied niches can be invaded causes occupied niches to be clustered in phenotype space and causes type I errors for cross-species analyses to increase as the maximum distance moved is decreased (see figure 4a for trees with 50 tips). Interestingly, the highest type I error for any given maximum distance is at an intermediate tree size. The reason for this is that with larger trees, more
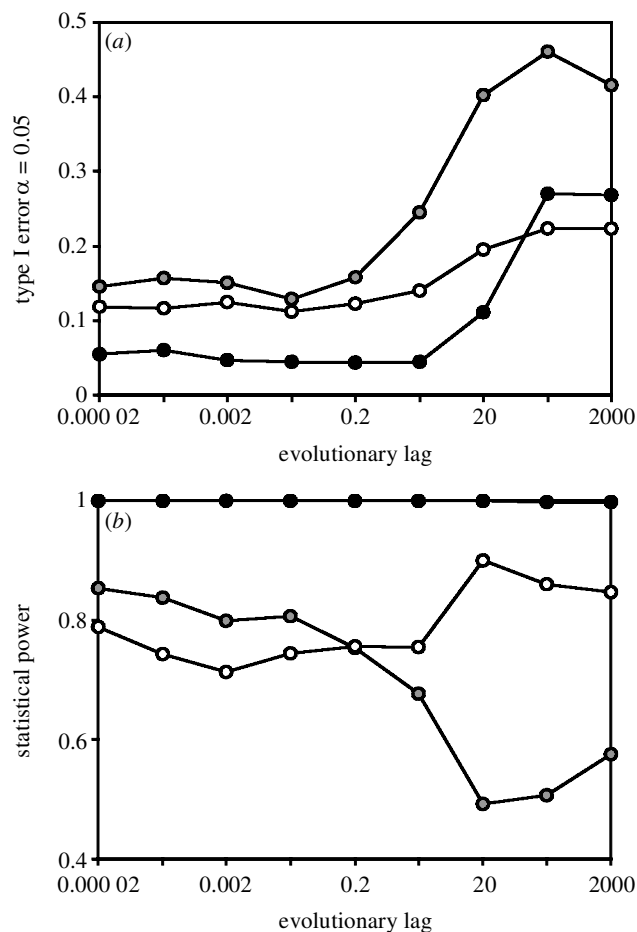
Figure 3. A total of 1000 trees with 50 tips were simulated for two conditions of character correlation (0.0 and 0.75) and nine levels of evolutionary lag (defined in § 3 (c)). In both (a) and (b), solid symbols refer to cross-species comparisons, grey symbols to time-scaled independent contrasts, and open symbols to independent contrasts with equal branch lengths. When evolutionary lag is small (0.00002), values for type I statistical error (a) and statistical power (b), which were both estimated as described for figure 2, approximate the values given for trees of size 50 in figure 2a,b, respectively.
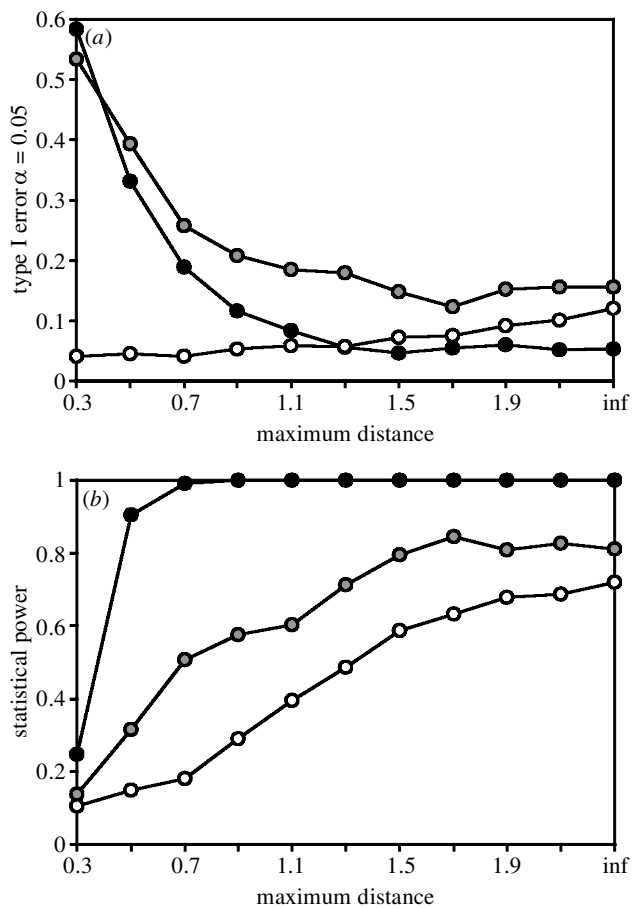
Figure 4. A total of 1000 trees with 50 tips were simulated for two conditions of character correlation (0.0 and 0.75) and 11 levels of maximum distance (defined in § 3(d)). In both (a) and (b), solid symbols refer to cross-species comparisons, grey symbols to time-scaled independent contrasts, and open symbols to independent contrasts with equal branch lengths. When maximum distance is infinite (inf), values for type I statistical error (a) and statistical power (b), which were both estimated as described for figure 2, approximate the values given for trees of size 50 in figure 2a,b, respectively.

cascades have occurred and a higher proportion of the bivariate phenotype space, dictated by the niche dimensions, has been occupied, so type I error rates are reduced. Statistical power in cross-species analyses is, unsurprisingly, higher for larger trees with greater allowed maximum distances (see figure 4b for trees with 50 tips). Again, time-scaled contrast analyses have somewhat higher type I error rates and appreciably less statistical power than cross-species analyses. Contrasts assuming equal branch lengths produce very low statistical type I error rates with short maximum distances because the contrast values fail to extract the relevant signal in the data: the statistical power for contrast analyses assuming equal branch lengths is very low indeed, and they perform even more poorly than time-scaled contrasts over all maximum distances.

For the simulations given in figure 4a, the diagnostic analyses were again effective. Significant correlations at the $p < 0.05$ level between the values of the contrasts and their standard deviations were found for all 1000 simula-

tions performed for each maximum distance (from 0.3 to infinity) with the use of both time-scaled standardized contrasts and equal-branch-length standardized contrasts.

(e) *Extinction*

So far we have considered a pure birth model in which all niches remain occupied once they have been invaded. However, under a Brownian-motion model of character evolution, type I errors are increased and statistical power is decreased for cross-species analyses when background extinction is introduced as a process (Harvey & Rambaut 1998). Introducing an extinction rate into the basic adaptationist model used in this paper, such that the probability of extinction of the species in a niche is independent of its position in niche space, does not alter type I errors or the power of cross-species statistical tests. The reason is that the bivariate normal distribution remains preserved.

There are two obvious models of extinction that might be incorporated. Recall that niches appear at a constant

rate per unit time but that the phylogeny is increasing in size through time, with the consequence that the rate of niche production for each lineage decreases as the number of niches increases. Niche extinction rate might be (i) set as Poisson distributed with a greater mean time between events than that for niche appearance, or (ii) set as density dependent so that the rate of extinction increases with the number of extant niches. In the former case, tree size will grow indefinitely, but in the latter an equilibrium will be reached when the rate of niche production and extinction for each lineage are the same.

4. NICHE-RELATED VERSUS BROWNIAN-MOTION PHENOTYPIC EVOLUTION

For the basic adaptationist model described in this paper, a phylogenetic tree has evolved in response to vacant niches arising. Each niche axis has an associated phenotype axis, and for each point in niche space there is an optimum phenotype. In the simulations, the two niche or phenotype axes have been uncorrelated ($r = 0$, for type I error analyses) or correlated ($r = 0.75$, for statistical power analyses). In the basic model, niches arose and were occupied according to a bivariate normal distri- bution and cross-species analyses had appropriate type I error when $r = 0$. However, when characters evolve from the root to the tips of a phylogenetic tree according to a Brownian-motion model of character evolution, we know that type I errors will be inflated (Martins & Garland 1991). This leads us to distinguish between two categories of characters: those associated with niche characteristics (N_i) under the model of adaptive radiation, and those that evolve by brownian motion (B_i). If there has not been correlated evolution between the niche characteristics or between the Brownian-motion characters, then what type I errors do we expect?

As discussed above, we know that type I errors for cross-species analyses between N_i will be appropriate, but those between B_i will be inflated. If the phylogeny were dependent on just one niche axis instead of two, the posi- tion of a pair of species with reference to others along the niche axis would be a good predictor of their phylogenetic relatedness: pairs of species which were each other's nearest neighbour would also share more recent common ancestry than either shares with any other species. When additional independent niche axes are added as phylo- genetic determinants, each will contribute less to tree structure. Shared evolutionary history between close rela- tives is the cause for inflated type I error of the estimated correlation between independently evolving B_i characters, and because N_i characters cause the shared evolutionary history we might expect to find inflated type I errors between B_i and N_i. However, as more niche axes contri- bute to tree structure, so differences between species on any one axis will be less accurate predictors of relatedness. Following that reasoning, we should expect type I error between a B_i and any particular N_i to decrease to nominal levels as the number of independent niche axes increases.

We performed a series of simulation studies in which between one and 100 independent niche axes were used to determine the multivariate normally distributed niche space. A total of 1000 trees with 50 species at their tips were generated for conditions with each of one, two, ten

Table 2. *The effect of the number of independent niche axes on an independently evolving Brownian-motion trait*

(A total of 1000 trees, each with 50 tips, were generated under the basic niche model with one, two, ten and 100 independent niche axes. After each tree had been simulated, two characters were evolved independently from root to tips according to a Brownian-motion model of morphological evolution, and the cross-species product moment correlation between them was calculated. One of those characters was then correlated with cross-species values for one of the niche variables.)

r between Brownian-motion variable and	type I error, $\alpha = 0.05$
independently evolving Brownian-motion variable	0.168
one niche axis of one	0.311
one niche axis of two[a]	0.260
one niche axis of ten[a]	0.137

[a] All niche axes are uncorrelated.

and 100 niche axes. Two characters were evolved from the root to the tips of each tree according to a Brownian- motion model of evolution. The characters were corre- lated with each other in a cross-species analysis, and then one of the characters (B_i) was correlated with a randomly chosen niche-dependent character (N_i). The results are given in table 2. The inter-B_i correlation has a type I error of three times the nominal value at $\alpha = 0.05$, as expected (Martins & Garland 1991; Harvey & Rambaut 1998). However, the type I error for the correlation between B_i and N_i is elevated, even with ten independent niche axes. This result points to the importance of under- standing the number of relevant niche dimensions as well as the expected mode of character evolution before performing comparative analyses. A pragmatic alterna- tive might be to perform the comparative analysis by using cross-species values, time-scaled independent contrasts and independent contrasts that assume equal branch lengths, and then test for normality of character state or contrast distributions as such, as well as normality of residuals from regression analyses.

5. A WAY FORWARD

Phylogenies show when, in relative or absolute time, pairs of species last shared common ancestry. Given a phylogeny and trait values, it is possible to estimate maximum-likelihood transformations of the phylogeny that would best account for the trait values. Such trans- formations might give insight into the way in which traits have evolved, and provide indications for appropriate analyses. Consider three examples. First, Pagel (1997) suggests a transformation of branch lengths, termed κ. Branch lengths are raised to the power κ, and if the maximum-likelihood value of κ is 1, then branch lengths are predictors of evolutionary change according to Felsenstein's Brownian-motion model of evolution, but if κ is 0, then all branches have equal length and a punctutational model may be more appropriate. Second, Grafen (1989) suggests (in a slightly different context) the transformation ρ, which is a power function that can be used to compress more recent branches and extend

deeper ones. Under Price's model, we expect less change to be apparent per branch length in more recent than in older branches. Third, Pagel (1997) has suggested to us the potential value of estimating a maximum-likelihood transformation λ, which is a multiple of internal branch lengths. If internal branch lengths are time-scaled by the multiple 0, then they do not exist (we have a star phylogeny) and a cross-species analysis is appropriate; however, if the estimate of λ is 1, internal branches are associated with the expected amount of evolution according to Felsenstein's Brownian-motion model. Judicious use of such maximum-likelihood estimators might well provide an appropriate way forward for determining how particular characters evolved, and for deciding the most appropriate method of comparative statistical analysis. The use of such measures will be explored elsewhere.

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