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Heterogeneous relationships between rates of speciation and body size evolution across vertebrate clades

Christopher R. Cooney[1*] **& Gavin H. Thomas**[1]

[1]*Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK.*

***Author for correspondence:** c.cooney@sheffield.ac.uk

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ABSTRACT

Several theories predict that rates of phenotypic evolution should be related to the rate at which new lineages arise. However, drawing general conclusions regarding the coupling between these fundamental evolutionary rates has been difficult, due to the inconsistent nature of previous results combined with uncertainty over the most appropriate methodology with which to investigate such relationships. Here we propose and compare the performance of several different approaches for testing associations between lineage-specific rates of speciation and phenotypic evolution using phylogenetic data. We then use the best-performing method to test relationships between rates of speciation and body size evolution in five major vertebrate clades (amphibians, birds, mammals, ray-finned fish, squamate reptiles) at two phylogenetic scales. Our results provide support for the longstanding view that rates of speciation and morphological evolution are generally positively related at broad macroevolutionary scales, but they also reveal a substantial degree of heterogeneity in the strength and direction of these associations at finer scales across the vertebrate tree of life.

INTRODUCTION

The rate at which new species arise and at which phenotypic traits evolve are two fundamental evolutionary rates[1,2], that, together, are thought to explain major patterns in the distribution of species richness and phenotypic diversity across the tree of life[3-6]. It has long been suspected that rates of speciation and phenotypic evolution may be correlated at macroevolutionary scales[1,7,8]. On the one hand, several long-standing evolutionary theories predict a positive coupling between these rates. Such theories include the concept of punctuated equilibrium[9] and the versatility hypothesis[10-12], where in the latter, increased phenotypic 'evolvability' promotes elevated rates of speciation by allowing diversifying lineages to utilise a broader spectrum of available resources. Similarly, a positive coupling between rates of lineage splitting and phenotypic (ecological) divergence is a fundamental component of adaptive radiation theory[13], and rapid phenotypic differentiation has been identified as an important feature of many celebrated evolutionary radiations (e.g. Hawaiian honeycreepers[14], Galapagos finches[15], cichlid fishes[16], *Anolis* lizards[17]).

On the other hand, there is growing evidence from a range of taxa that lineage diversification often proceeds without substantial phenotypic evolution, challenging the notion that phenotypic differentiation is a requirement for the origin and build-up of species diversity in evolutionary radiations[18-22]. For instance, studies integrating both ecological and evolutionary information have documented several examples of 'non-adaptive radiation' in a range taxa including snails, salamanders, birds, lizards and plants[18] in which lineage diversification has seemingly proceeded with minimal ecological divergence. Examples such as these are at odds with the notion of a general coupling between speciation and phenotypic divergence, and therefore challenge the expectation for widespread positive relationships between rates of speciation and phenotypic evolution at macroevolutionary scales.

To date, several studies have attempted to resolve these issues by testing for associations between per-lineage rates of speciation and phenotypic evolution estimated using phylogenetic data. However, such tests have found mixed results[23-36], ranging from strong positive associations between speciation and phenotypic evolution in some groups (e.g. ray-finned fishes[24]) to no relationship in others (e.g. birds[36]), making broad conclusions difficult to draw. A further complicating factor is that previous studies have addressed these questions using a range of different methodologies, making it difficult to assess whether the signal of inconsistent relationships across groups is real, or at least partly caused by methodological differences between studies. Indeed, as yet there has been no direct assessment of the relative strengths and weaknesses of different approaches for testing associations between speciation and phenotypic rates derived from phylogenetic data.

Here we address these issues in two ways. First, we use simulated datasets to conduct a systematic assessment of the accuracy and performance of different approaches for testing correlations between phylogenetic rates of speciation and trait evolution under a range of simulated conditions. In particular, we focus on assessing the potential for trait measurement error to mislead such tests, as this issue has previously been shown to cause biases in models of trait evolution[37-39] that could negatively impact tests of the relationship between speciation and trait evolution[40]. Second, using the best-performing approach, which we refer to as the Correlated Speciation and Trait Rates Simulation (Cor-STRATES) framework, we test longstanding hypotheses for the relationship between rates of speciation and morphological (body size) evolution in five major vertebrate taxa (amphibians, birds, mammals, ray-finned fish, squamate reptiles). Together these clades encompass >63,000 species spanning over 450 million years of evolutionary history, and in each case we examine relationships at both the whole-clade level and between major subclades within each group. This two-scale approach, combined with the application of a single robust methodological framework throughout, provides insight into the relationship between two fundamental macroevolutionary rates across a major section of the tree of life.

RESULTS

Performance of evolutionary rate models. We tested the accuracy and performance of two methods for estimating per-lineage speciation rates (BAMM[41], DR[4]) and four methods for estimating per-lineage rates of trait evolution (BAMM[24], BayesTraits[5], StableTraits[42], mvBM[43]). For speciation rates, we found that BAMM consistently outperformed DR for all but the smallest tree sizes (50 tips), generating speciation rate estimates that were more accurate, less biased and more strongly correlated with true (i.e. simulated) rates (Extended Data Figure 1). This was the case regardless of whether we compared BAMM speciation rates across all branches in the tree or for terminal branches (i.e. tips) only (Extended Data Figure 1). For trait rates, we found that BAMM and BayesTraits outperformed StableTraits and mvBM, providing more accurate (absolute) rate estimates that were considerably more strongly correlated with true rates, particularly in larger trees (100-500 tips; Extended Data Figure 1). Based on these results, we focused our subsequent performance analyses on speciation rates estimated by BAMM (λ_{BAMM}) and trait rates estimated by either BAMM (σ^2_{BAMM}) or BayesTraits (σ^2_{BT}).

Testing associations between rates of speciation and trait evolution. We used simulated 250-tip datasets exhibiting positive, negative, and no coupling between rates to test the performance of four different approaches for inferring the correct association between rates of speciation and trait evolution (Figure 1 and Extended Data Figure 2). The best performing approach (simulation + tree-rescaling) consisted of an initial tree-scaling step using Pagel's lambda[44] to adjust for the extent of phylogenetic signal in the trait data, followed by a simulation-based significance test whereby the observed correlation between rates is compared to a null distribution of correlations generated by evolutionary simulation (Figure 2). This approach had good power to detect both positive and negative associations between speciation and trait rates, regardless of whether trait rates were estimated with BayesTraits (Figure 1) or BAMM (Extended Data Figure 2). Importantly, Type I error (false discovery) rates remained consistently low (~5%), even in the presence of considerable trait measurement error. The same outcomes were not observed for the three other approaches we investigated (PGLS only, PGLS + tree-rescaling, simulation only), which exhibited reduced statistical power and/or unacceptably high Type I error rates, particularly with measurement error in trait values (Figure 1 and Extended Data Figure 2).

Focusing on this best-performing approach, which we refer to as the Cor-STRATES framework (Figure 2), we found that comparing per-branch rates across all branches in the tree and at the tips only showed similar performance, whereas a weighted-averaging approach incorporating information from deeper branches but weighted towards the tips slightly underperformed relative to the other two approaches (Extended Data Figures 2 and 3). We also found that in the context of testing for relationships with speciation rates, trait rates derived from BayesTraits (σ^2_{BT}) (Figure 1) generally lead to better performance than trait rates derived from BAMM (σ^2_{BAMM}) (Extended Data Figure 2). A further comparison of effect sizes showed that BayesTraits rates generally gave larger average effect sizes than BAMM rates, particularly in scenarios involving negative associations between rates (Extended Data Figure 3). Although the differences in performance between BayesTraits and BAMM are marginal, we therefore conducted all subsequent analyses using trait rates derived from BayesTraits (σ^2_{BT}). However, we acknowledge that alternative scenarios not considered here may favour alternative frameworks.

Further testing using the Cor-STRATES framework showed that the power to detect significant associations between rates unsurprisingly depends on tree size and simulated correlation strength (Extended Data Figure 4), ranging from low power (~0.1) in small datasets (50 tips) to very high power (~1.0) in large datasets (500 tips) simulated with strong correlations between rates (see Methods). These results also showed that trait measurement error reduced the power to detect significant associations between speciation and trait rates, but that this reduction disproportionately effects the detection of negative relationships relative to positive ones (Extended Data Figure 4). Importantly, Type I error rates remained acceptably low (~5%) at all tree sizes, irrespective of the level of measurement error in trait values.

We also investigated the impact of incomplete species sampling and non-zero turnover (relative extinction) rates on test performance. Predictably, we found that the power to detect significant associations fell as the proportion of missing species increased (Extended Data Figure 5), but only declined to very low levels under the most extreme combinations of trait measurement error and sampling incompleteness (i.e. 75% of species missing from a 250-tip tree). For turnover, we found that when trait measurement error was absent, non-zero relative extinction rates had relatively little impact on the power to detect either positive or negative associations between rates (Extended Data Figure 6). In fact, we found that power marginally increased under these scenarios relative to base levels (Extended Data Figure 6), which may reflect to some extent relatively unusual shape of trees generated assuming increasingly high rates lineage turnover. In scenarios involving trait measurement error, however, we found that lineage turnover disproportionately reduced the power to detect negative associations between rates, particularly under very high turnover levels (0.9), whereas the power to detect positive associations was relatively unaffected (Extended Data Figure 6). Lineage turnover had no effect on Type I error rates, however, which remained acceptably low in all cases.

Relationships between speciation and body size evolution in vertebrates. We used the Cor-STRATES framework (Figure 2) to test the coupling between rates of speciation and body size evolution in five major vertebrate groups: amphibians (sampled / total richness = 3,193 / 7,238 spp.), birds (6,670 / 9,993 spp.), ray-finned fish (10,868 / 31,516 spp.), mammals (4,095 / 5,561 spp.) and squamate reptiles (5,398 / 9,755 spp.) (Supplementary Data 1). Comparing speciation rates estimated by BAMM (λ_{BAMM}) to body size rates estimated by BayesTraits (σ^2_{BT}) (Figure 3), our tests revealed consistently positive relationships between rates of speciation and body size evolution across the five groups that were significantly more extreme than expected based on null simulations (Figure 4). The strength of the association between rates varied between groups, however, ranging from an effect size (observed ρ – simulated ρ) of 0.15 [95% CI: 0.06, 0.24] in birds to 0.47 [95% CI: 0.39, 0.57] in squamates (Extended Data Figure 7). These results correspond to correlations based on tip rates, but tests based on rate variation across all branches in the tree gave similar results (Extended Data Figure 7).

To further investigate the extent of among-clade variability in the coupling between speciation and body size evolution, we also tested relationships separately for major subclades within each of the five groups. Focusing largely on recognised subclades (usually orders or families) containing >100 species with trait data and for which satisfactory convergence of rate models could be achieved (*n* = 65 clades), we found that relationships between speciation and trait rates varied considerably between subclades (Figure 5; Extended Data Figure 8), despite overarching positive relationships. For example, focusing on results based on tip rates, effect sizes for individual subclades ranged from 0.69 [95% CI: 0.19, 1.10] in shorebirds (Order: Charadriiformes) to -0.56 [95% CI: -0.97, -0.17] in toads (Family: Bufonidae). Results were generally similar when tests were conducted using rates extracted from all branches in the tree (Figure 5). Overall, 15 out of the 65 subclades exhibited significant associations between rates of speciation and body size evolution in at least one of the comparisons, representing 13 positive associations and 2 negative associations (Supplementary Data 2).

Using Bayesian phylogenetic mixed models, we found that variation in effect size scores across individual subclades was largely unrelated to differences in crown age (Myr), total species richness, sampling proportion, the degree of phylogenetic signal in body size values and the variance in per-branch rate estimates within clades. Specifically, we found some limited evidence that absolute effect size was related to species richness and the extent of within-clade variance in speciation rates (i.e. stronger relationships in more species-rich clades and those with greater variance in speciation rates), but these relationships were weak and highly inconsistent across datasets (Extended Data Figure 9).

DISCUSSION

Here we have developed an approach for testing associations between rates of speciation and phenotypic evolution using phylogenetic data – the Cor-STRATES framework – and used it to robustly test longstanding theories concerning the coupling between rates of speciation and morphological evolution at macroevolutionary scales. Focusing on the relationships between speciation rates and rates of body size evolution, we found strong evidence that these fundamental evolutionary rates are positively correlated in five major vertebrate clades (amphibians, birds mammals, ray-finned fish, squamate reptiles). Analysing these relationships at a finer phylogenetic scale (i.e. among subclades within the five main groups) revealed evidence for more extensive variation in the coupling between speciation and body size evolution, but where significant relationships were inferred, most clades (13 out of 15) exhibited positive associations.

These results have several important implications. First, as we found significant positive associations between rates in each of the five groups tested, our results suggest that a positive coupling between speciation and morphological evolution represents a general feature of vertebrate evolution. Previous studies investigating these relationships at a similar phylogenetic scale in select vertebrate groups have reached mixed conclusions (e.g. birds[26,36], mammals[5,35]). As a result, broad insights concerning the nature of the relationships between speciation rates and rates of morphological evolution in these groups and in vertebrates more generally remained difficult to draw. Our results, based on the application of a consistent methodological framework to each of the five groups, bolster support for the existence of positive relationships between evolutionary rates in these taxa, in line with the idea that positive correlations between rates speciation and morphological evolution have played an important role in shaping the vast majority of vertebrate diversity[24].

Several explanations have been proposed to explain positive correlations between rates of speciation and morphological evolution at macroevolutionary scales. For instance, adaptive radiation theory predicts a co-incidence between the evolution of ecological diversity and rapid lineage splitting, as lineages rapidly ecologically differentiate to fill unoccupied niche space[13]. These ideas are closely related to the notion of morphological evolvability or 'versatility' promoting accelerated speciation rates, in the sense that enhanced rates of morphological change facilitates rapid species accumulation by allowing lineages to diversify to utilise a broader spectrum of available resources[10,11]. Similarly, mechanisms associated with the more traditional concept of punctuated equilibrium (i.e. phenotypic change concentrated largely at speciation events) also predict a general positive coupling between speciation rates and rates of morphological evolution, albeit with the opposite direction of causality (i.e. the speciation process itself drives rapid morphological change[9]). Separating these alternative interpretations based on correlations between evolutionary rates remains difficult[45], but irrespective of the underlying mechanism, broad positive relationships between rates of speciation and body size evolution imply a central role for morphological evolution in facilitating diversification in evolutionary radiations[24].

However, an important additional feature of our results is that despite these overarching relationships, there appears to be considerable variation in the strength of coupling between rates of speciation and body size evolution both within and between vertebrate radiations. For instance, at the whole-clade level, we found a much tighter relationship between rates of speciation and body size evolution in squamate reptiles than in the other four groups. Counter-intuitively, the relatively strong whole-clade correlation in squamates is not reflected by within-clade trends, that are significantly positive for only one clade (Colubridae). This indicates that rates of speciation and trait evolution may often be decoupled, or show idiosyncratic trends, at comparatively fine phylogenetic scales but that clade-specific factors could simultaneously drive changes in rates of both speciation and trait evolution at broader scale. Indeed, at finer phylogenetic scales, our subclade analyses revealed considerable variation in the coupling between rates of speciation and body size evolution between major subclades within each of the five radiations. At least some of this variation in effect strength between clades (particularly at the subclade level) may simply reflect variation in statistical power relating to clade size (see Extended Data Figure 4) or species sampling (see Extended Data Figure 5), and other issues connected to the extent of 'arbitrariness' with which the taxonomic units we study are defined (i.e. Simpson's paradox[46,47]). However, at least some of this variation may be indicative of differences in the relative importance of particular speciation processes driving speciation among taxa. For instance, we found strong positive associations between rates of speciation and body size evolution in several subclades in which it has been argued that size differentiation has played a major role in facilitating species diversification [e.g. cichliform fish[48,49] (Cichliformes), bats[50,51] (Chiroptera), colubrid snakes[52] (Colubridae) and shorebirds[53] (Charadriiformes)].

In contrast, we identified a small number of clades – namely, toads (Bufonidae) and lacertid lizards (Lacertidae) – in which speciation rates were negatively (i.e. inversely) related to rates morphological evolution, in line with previous results implying a strong connection between lineage splitting and relative morphological stasis in these groups[54-57]. The existence of 'inverted' relationships between speciation and morphological rates such as these are intriguing, because they suggest that the processes driving speciation in these groups are deterministically different to the processes dominating in other subclades and over broader phylogenetic and temporal scales more generally. In particular, negative associations between speciation rates and rates of body size evolution are consistent with diversification via so-called 'non-adaptive radiation', in which lineage splitting is primarily driven by factors such as geographic isolation and/or mating differentiation, with little morphological or ecological differentiation among taxa[18-20,22]. However, it may be that diversification in ecomorphological traits other than body size have been important in facilitating speciation in these groups (see below). Nonetheless, this heterogeneity between subclades can also help to explain the generally 'noisy' positive relationships between speciation rates and rates of body size evolution when viewed at broader phylogenetic scales (i.e. Figure 3).

It is important to note that these conclusions are subject to other potential caveats. For instance, our approach does not bypass general issues concerning our ability to accurately estimate evolutionary rates (speciation and trait evolution). Indeed, such rates are intrinsically difficult to estimate based on phylogenetic data alone, particularly over deep timescales[58] and when rate shifts involves slow-downs rather than speed-ups in rate[59]. It is therefore likely that such issues weaken our ability to detect tight couplings between evolutionary rates. However, our performance analyses allowed us to select rate modelling frameworks with the highest degree of accuracy among those that we were able to test, and by predominately focusing on tip rates (i.e. the most recent branches of the phylogeny), our approach should maximise our ability to infer accurate relationships between evolutionary rates. More generally, although our analyses allowed us to identify a seemingly robust framework for testing correlations between speciation and phenotypic rates, future analyses may wish to refine our general workflow (Figure 2) by factoring in more powerful rate models and/or more precise information concerning potential sources of error, as the necessary methods and data become available. In particular, we note that our current approach does not explicitly account for lineage-specific variation in trait measurement error, nor other potentially important sources of bias, such as systematic error in phylogenetic branch lengths, which has the potential to bias estimates of both speciation and trait rates. Finally, our own performance analyses clearly show that it is generally harder to detect negative associations between rates of speciation and trait evolution than positive ones – particularly in situations with considerable trait measurement error, reduced species sampling and/or high relative extinction. Thus, negative associations between speciation and morphological evolution may be more common than our results imply and so may be more widespread in nature than currently recognized.

Furthermore, it is worth noting that the coupling between rates of speciation and phenotypic evolution may also depend on the identity of the particular trait(s) being studied. Here we focus on body size, under the assumption that evolutionary changes in size (or lack thereof) are informative about the processes driving speciation in these lineages. Body size is strongly correlated with many important aspects of organismal biology (e.g. habitat, life history, trophic position[60]) and divergence in body size has been linked to ecological differentiation and reproductive isolation in a variety vertebrate lineages[15,21,61]. However, in many cases speciation may depend more strongly on divergence in traits other than body size, that are more closely connected to ecological differentiation and/or reproductive isolation among lineages. For example, it is possible that divergence in ecomorphological traits such body shape or environmental niche traits such as climate or habitat type are characterised by contrasting relationships with speciation rates than we find here for body size. Likewise, studying traits more directly relevant to mate choice and species recognition (e.g. sexual signalling traits[62,63]) may also provide more direct insight into the role of reproductive isolation in determining variation in speciation rates at macroevolutionary scales[64].

Overall, our results in relation to body size evolution support longstanding predictions for a consistent positive coupling between rates of speciation and morphological divergence at broad macroevolutionary scales[1,2,7]. At the same time, however, they reveal evidence for considerable variability in the association between these evolutionary rates in different parts of the vertebrate radiation, consistent with the general idea that the relative importance of processes driving speciation – such as adaptive and non-adaptive radiation – varies across the tree of life[18]. Our multi-predictor models of subclade effect sizes suggested that this variation in the coupling between rates is unrelated to both clade age and species richness, as may be expected if macroevolutionary rates change in concert over time[65] or if factors such as branch length error simultaneously bias estimates of clade age and speciation and phenotypic rates within clades[66]. Thus, the 'predictability' of clade-specific relationships between speciation and phenotypic evolution remains to be determined, but factors such as ecological opportunity[13,67], sexual selection[22,68] and dispersal ability[69,70] may deterministically increase the potential for positive and negative rate-relationships, respectively. Nonetheless, our study sheds light on the association between rates of speciation and morphological evolution at broad phylogenetic scales and provides a promising framework for testing relationships between speciation and phenotypic evolution using phylogenetic data.

METHODS

Rates of speciation. We investigated the performance of two different approaches for inferring variation in per-lineage rates of speciation: BAMM[41] (version 2.5.0) and DR[4]. BAMM uses a Bayesian model-based approach to estimate speciation (and extinction) rates across the tree, under the assumption that phylogenetic diversification dynamics can be approximated by a set of discrete rate regimes. In contrast, the DR statistic is a model-free tip rate metric that incorporates information on the number of splitting events and internode distances along a root-to-tip path of a phylogeny (weighted toward the present) to provide a measure of recent lineage-specific speciation rate[71]. We focused on these two approaches because they are capable of providing lineage-specific speciation rate estimates and in the case of DR have been shown to outperform other related approaches (e.g. the node density metric[72]). We did not explore the performance of ClaDS[73], another recently developed model-based method, because we found that it was computational unfeasible to fit this model to either our simulated or empirical datasets. We acknowledge however that the ClaDS method can outperform both DR and (more marginally) BAMM in accurately reconstructing simulated patterns of speciation rate variation across phylogenies in some diversification scenarios[73].

To fit BAMM diversification models to our datasets (simulated and empirical), we used default priors generated by the 'setBAMMpriors' function in BAMMtools[74]. The only exception to this was that in all cases we set the 'expectedNumberOfShifts' prior to be proportional to the number of tips in the phylogeny. We adjusted MCMC run length according to tree size, using iteration lengths of 2 million (250 tips or less) or 5 million (500 tips) for simulated datasets, and 20 million (<500 tips), 50 million (500-1000 tips) or 100 million (>1000 tips) for empirical vertebrate datasets (see below). For analyses based on simulated datasets we took 2,000 samples from the posterior, and for vertebrate analyses we took 10,000 samples. Runs were checked for satisfactory convergence and in all cases we discarded the first 20% of sampled iterations as burn-in. Mean per-branch speciation rates were estimated using the 'getMeanBranchLengthTree' function in BAMMtools, and DR values were estimate using the equations provided in ref. [4].

Rates of trait evolution. We investigated the performance of four different approaches for reconstructing patterns of trait rate heterogeneity, each of which have been used to infer per-lineage rates of trait evolution in empirical datasets: (i) BAMM[24], (ii) the BayesTraits (version 3) variable rates model[5], (iii) the StableTraits model[42], (iv) the 'mvBM' method[43] implemented in the R package 'evomap'. BAMM and BayesTraits both use Bayesian model-based approaches to estimate shifts in rates of evolution across a phylogeny, though the manner in which rate shifts are modelled differs between the methods. Specifically, BAMM models discrete shifts for a node and all of its descendants and allows rates to vary through time. BayesTraits also models discrete shifts for a node and all of its descendants and also explicitly allows discrete shifts on single internal branches, but does not model temporal rate variation (see ref. [75] for a more comprehensive overview). In contrast, StableTraits and mvBM are primarily geared toward ancestral states inference but estimates of per-lineage evolutionary rate emerge as a consequence of the inferred pattern of trait change between ancestral and descendent nodes in the tree. StableTraits draws increments in evolving characters from a heavy-tailed stable distribution so that trait evolution is modelled as a mixture of background gradual change interspersed with occasional large jumps[42]. Finally, mvBM is a method that deterministically calculates branch-specific rates of evolution and uses those estimates to parameterize a multivariate BM which is then used to infer ancestral trait values. Collectively these four methods are used extensively to study phylogenetic patterns of trait evolution [e.g. refs. [3,5,24,32,76-78]], yet their relative performance and accuracy for correctly inferring rate heterogeneity across phylogenies has not been systematically assessed (though see ref. [75]).

To fit BAMM trait models we used the same approach as we used for estimating speciation rates (see above). We used the same MCMC run settings to fit the BayesTraits variable rates model, using default priors in all cases. StableTraits models were run for 1 million iterations (sampling every 500 iterations), which was sufficient to achieve model convergence in all cases. As above, for BAMM we estimated mean per-branch evolutionary rates using the 'getMeanBranchLengthTree' function in BAMMtools. For the other models, we calculated per-branch estimates of evolutionary rate by dividing output tree branch lengths (which are set proportion to the estimated degree of evolutionary change on each branch) by the corresponding branch lengths of the time-calibrated input tree[3,79].

Simulating patterns of trait rate-dependent speciation. We evaluated the ability of various approaches to infer true relationships between speciation rates and trait rates (see below) by assessing their performance on trees simulated using ClaDS[73]. The ClaDS model considers a birth-death diversification process in which diversification rates (speciation and extinction) are inherited along lineages but change stochastically at speciation events, shifting to new values drawn from a specified distribution centred on ancestral values. As mentioned above, this approach performs well at inferring both small and large changes in diversification rates[73], and for our purposes provides a useful approach for simulating phylogenies exhibiting patterns of speciation rate heterogeneity. We used the 'sim_ClaDS' function in RPANDA[80] to simulate phylogenetic trees of different sizes under the default ClaDS model in which new speciation rates are drawn from a lognormal distribution with mean = $\alpha^*\lambda$ and variance = σ^2, where λ is the ancestral speciation rate and α is a trend parameter. We simulated trees with 50, 150, 250 and 500 tips (100 trees in each case) using the following parameters $\lambda_0 = 0.1$, $\sigma = 0.175$, $\alpha = 1$, $\varepsilon = 0$, where λ_0 is the initial speciation rate and ε is the turnover (extinction/speciation) rate (i.e. extinction rate = 0). We also simulated an additional set of 250-tip trees with low ($\varepsilon = 0.1$) and high ($\varepsilon = 0.9$) turnover rates to allow us to assess the impact of extinction on model performance.

For each simulated tree we extracted values for the realised speciation rate of each branch and used these values to calculate branch-specific trait rates that were positively, negatively or uncorrelated with speciation rates. For scenarios involving correlated rates, we generated branch trait rates that were strongly ($r = \pm1$) or more weakly ($r = \pm0.5$) associated with speciation rates. We note, however, that due to the stochastic nature of the trait simulations (see below), the realised correlation between speciation and trait rate heterogeneity in our simulated datasets is always lower than implied by the strength of the correlation between branch rates in the generating model (see Extended Data Figure 10 for estimates of realised correlation strengths). For uncorrelated scenarios, we used two different approaches to generate uncorrelated trait rates: first we simply constrained trait rates to be constant across the tree, and second we generated variable trait rates across the tree that were random with respect to speciation rates. This allowed us to explore the impact of two different forms of uncorrelated trait rates on model performance (i.e. constant and variable rates). To generate trait values based on these patterns of rate heterogeneity, we simulated trait values using a Brownian motion model applied to the appropriate rate-scaled trees[75,81]. While this approach does not constitute a formal process-based simulation procedure, whereby trait rates are directly linked to speciation rates, it is capable of generating patterns consistent with a process of trait rate-dependent speciation.

Finally, to explore the impact of trait measurement error on the inference of speciation rate-trait rate correlations, for each set of simulated trait values described above, we generated two additional sets of tip values representing average measurement error of 1% and 10% of the standard deviation of the original set of trait values.

Testing the accuracy of evolutionary rate models. To investigate the relative performance of our focal rate models, we applied each model to a subset of our simulated trees and compared the accuracy of the resulting rate estimates to the true (i.e. generating) values. Specifically, we fit the two speciation rate (BAMM and DR) and four trait rate methods (BAMM, BayesTraits, StableTraits, mvBM) to simulated datasets with 50, 150, 250 and 500 tips (without extinction and measurement error; *n* = 100 trees in each case). We then assessed accuracy using two measures of error (mean absolute error and mean proportional error; for equations see ref. [71]) and by calculating the correlation (Pearson's *r*) between true and estimated rates.

Exploring alternative rate summary statistics. We explored three different approaches for summarising rate heterogeneity that differ in the extent to which they incorporate information from deeper branches. First, we compared per-branch speciation and trait rates across all branches in the tree. Second, we compared per-branch rate variation among terminal branches (tips) only. Finally, we examined the performance a recently-developed metric for summarising rate variation at the tips of the tree. This metric, called TR by Cooney *et al.* [ref. [63]], uses a weighted-averaging approach to summarise rate variation from the full root-to-tip path for each tip, while weighting values towards variation at the tips of the tree. The input for this approach is a tree with branch lengths in units of (mean) evolutionary rate, therefore it can be used to summarise variation in both trait and speciation rates, using mean rate trees as input in each case. We compared the performance of these three summary approaches (i.e. all branches, tips only and weighted-average) for detecting relationships between rates of speciation and trait evolution from phylogenetic trees.

Significance tests. We compared the performance of two distinct approaches for inferring the significance of associations between speciation and trait rates: (i) phylogenetic generalised least-squares (PGLS) regression and (ii) a simulation-based test where the observed correlation between rates is compared to a null set of correlations generated by simulation. PGLS models were fit using the 'phylolm' function in phylolm[82], assuming an optimised lambda model for the error structure. For the simulation-based test, we simulated sets of trait values (*n* = 100 or 200 for simulated and vertebrate datasets, respectively) based on a Brownian motion (BM) null model, utilising the diffusion rate (σ^2) parameter from a maximum likelihood fit of the BM model to the observed trait data. We then re-estimated trait rates for each null dataset, using run lengths of 500,000 (250 tips or less) or 1,250,000 (500 tips) for simulated datasets, and 2 million (<500 tips), 5 million (500-1000 tips) or 10 million (>1000 tips) for empirical vertebrate datasets, taking 1,000 (simulated datasets) or 2,000 (vertebrate datasets) posterior samples in each case. We then compared mean trait rates for each null simulation to observed speciation rates and used the resulting distribution of correlation coefficients to compute a two-tailed *P* value for the observed correlation coefficient[83]. We used Spearman's rank correlation (ρ) to measure the association between rates because the distribution of estimated speciation and/or trait rates is often highly non-normal, even after log-transformation, which makes applying parametric statistics such as Pearson's *r* problematic.

In combination with these two approaches, we also explored the impact of controlling for the observed level of phylogenetic signal in the trait data prior to estimating trait rates, by first rescaling the empirical phylogeny by the estimated value of Pagel's lambda[44]. Measurement error and other sources of non-phylogenetic trait variation (e.g. intra-specific variation) can generate biases in estimates of trait evolutionary rates, particularly for short branches[84], potentially leading to spurious correlations between trait rate metrics and speciation[40]. However, rescaling branch lengths by an appropriate value of lambda (estimated using the empirical time tree and the trait data) prior to estimating trait rates may account for (or at least mitigate) this bias, and in turn reduce the potential for spurious correlations between rates. We therefore combined this tree-rescaling step with each of the significance tests described above to generate four distinct approaches for testing the association between speciation and trait evolution: (i) PGLS only, (ii) PGLS + tree-rescaling, (iii) simulation only, (iv) simulation + tree-rescaling. (Note: the tree-rescaling is only used in relation to rates of trait evolution; speciation rates are always calculated using the original, time-calibrated phylogeny; see Figure 1).

Performance tests. We assessed the ability of different approaches to detect the correct association between rates of speciation and trait evolution by applying each method to simulated datasets of 250-tip trees generated assuming positive, negative and no correlation between rates, and with varying degrees of trait measurement error (0%, 1%, 10%). For each scenario, we counted the proportion of times (out of 100) a given method inferred a significant ($P < 0.05$) association between rates. Following this initial assessment, we then applied the best-performing method (simulation + tree-rescaling; see Results) to a broader range of simulated scenarios to explore changes in power and false discovery rates associated with varying tree sizes, sampling proportions, and extinction (turnover) rates.

Vertebrate analyses. We investigated relationships between rates of speciation and body size evolution in five vertebrate clades with good data on body size and phylogeny: amphibians, birds, mammals, ray-finned fish and squamate reptiles. Phylogenetic data came from recent, time-calibrated molecular phylogenies for each group[4,6,85-87]. Because the evolutionary rates models we use are computationally expensive to fit (particularly to large phylogenies), our analyses are based on a maximum clade credibility (MCC) tree for each group, generated in each case using the 'maxCladeCred' function in phangorn[88] and based on 1,000 trees sampled at random from the posterior distribution. To ensure reliable estimates of evolutionary rates[84], our analyses only include species placed in phylogenies using genetic data. For speciation rate analyses using BAMM, we included information on the proportion of sampled species in each analysis compared to the corresponding taxonomy associated with each phylogeny (for values see Extended Data Figure 7 and Supplementary Data 2). Body size information for each group was compiled from various sources: for birds[89] and mammals[86] we used estimates of species' mean body mass (g), whereas for amphibians[90,91], fish[92] and squamates[93] we used estimates of species' maximum length (mm). Size maxima are good proxies of body size in species with indeterminate growth[93], as in common in amphibians, fish and reptiles, and despite downsides related to comparability among species with different body plans, we focused on length measurements for these groups as they are by far the most readily available data in the literature. In each case, size values were $\log_{10}$-transformed prior to rate model fitting. The full size dataset is provided in Supplementary Data 1.

We performed two sets of analyses on our vertebrate datasets using the best-performing method identified by our performance analyses (simulation + tree-scaling). First, we tested the association between rates of speciation and body size evolution at the whole-clade level. Second, we assessed the extent of intra-group variation in speciation rate-body size rate relationships by running separate analyses on subclades within each group that contained 100 or more sampled species. In most cases, these subclades corresponded to recognised taxonomic units within each group (e.g. orders, families), with the exception of a small number of fish taxa that have recently been found to be non-monophyletic[6] (see Supplementary Data 1 for clade designations). In each case, effect sizes describing the strength and direction of the inferred relationship were was calculated as either ρ_{obs} – mean(ρ_{null}) giving the unstandardised effect size, or ρ_{obs} – mean(ρ_{null}) / sd(ρ_{null}) giving the standardised effect size.

Finally, we tested whether variation in subclade effect size estimates was related to differences in among clades in taxonomic richness and/or crown age (Myr; extracted from MCC trees), whilst also controlling for differences in sampling rates, the degree of phylogenetic signal in body size values, and the extent of within-clade variance in speciation and body size rate estimates, measured as the coefficient of variation (CV) for log-normal data:

$$CV = \sqrt{e^{\sigma^2} - 1}$$

, where σ^2 is the variance of per-branch rate estimates. To do this, we ran multi-predictor Bayesian phylogenetic mixed-models using the MCMCglmm[94] R package and the backbone tree illustrated in

Figure 3. We used uninformative priors and included as random effects both the phylogenetic co-variance matrix and a variable denoting whether mass or length estimates were used to test the relationship between body size and speciation rates. Models were run with the following settings: nitt = 1,100,000, burnin = 100,000, thin = 200 and all models showed suitable convergence.

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REFERENCES

1 Simpson, G. G. *The major features of evolution*. (Columbia University Press, 1953).

2 Simpson, G. G. *Tempo and mode in evolution*. (Columbia University Press, 1944).

3 Cooney, C. R. *et al.* Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature* **542**, 344-347, (2017).

4 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444-448, (2012).

5 Venditti, C., Meade, A. & Pagel, M. Multiple routes to mammalian diversity. *Nature* **479**, 393-396, (2011).

6 Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392-395, (2018).

7 Stanley, S. M. *Macroevolution: pattern and process*. (Freeman, 1979).

8 Reznick, D. N. & Ricklefs, R. E. Darwin's bridge between microevolution and macroevolution. *Nature* **457**, 837-842, (2009).

9 Gould, S. J. & Eldredge, N. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* **3**, 115-151, (1977).

10 Vermeij, G. J. Biological versatility and earth history. *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1936-1938, (1973).

11 Vermeij, G. J. Adaptation, versatility, and evolution. *Systematic Zoology* **22**, 466-477, (1973).

12 Liem, K. F. Biological versitility, evolution, and food resource exploitation in African cichlid fishes. *Am. Zool.* **15**, 427-454, (1975).

13 Schluter, D. *The ecology of adaptive radiation*. (Oxford University Press, 2000).

14 Lovette, I. J., Bermingham, E. & Ricklefs, R. E. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proc. R. Soc. London Ser. B* **269**, 37-42, (2002).

15 Grant, P. R. & Grant, B. R. *How and why species multiply: the radiation of Darwin's finches*. (Princeton University Press, 2008).

16 Danely, P. D. & Kocher, T. D. Speciation in rapidly diverging systems: lessons from Lake Malawi. *Mol. Ecol.* **10**, 1075-1086, (2001).

17 Losos, J. B. *et al.* Niche lability in the evolution of a Caribbean lizard community. *Nature* **424**, 542-545, (2003).

18 Czekanski-Moir, J. E. & Rundell, R. J. The ecology of nonecological speciation and nonadaptive radiations. *Trends Ecol. Evol.* **34**, 400-415, (2019).

19 Rundell, R. J. & Price, T. D. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends Ecol. Evol.* **24**, 394-399, (2009).

20 Svensson, E. I. Non-ecological speciation, niche conservatism and thermal adaptation: how are they connected? *Organisms Diversity & Evolution* **12**, 229-240, (2012).

21 Wollenberg Valero, K. C. *et al.* Patterns, mechanisms and genetics of speciation in reptiles and amphibians. *Genes* **10**, 646, (2019).

22 Mendelson, T. C., Martin, M. D. & Flaxman, S. M. Mutation-order divergence by sexual selection: diversification of sexual signals in similar environments as a first step in speciation. *Ecol. Lett.* **17**, 1053-1066, (2014).

23 Rabosky, D. L. & Adams, D. C. Rates of morphological evolution are correlated with species richness in salamanders. *Evolution* **66**, 1807-1818, (2012).

24 Rabosky, D. L. *et al.* Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature communications* **4**, 1958, (2013).

25 Gomes, A. C. R., Sorenson, M. D. & Cardoso, G. C. Speciation is associated with changing ornamentation rather than stronger sexual selection. *Evolution* **70**, 2823-2838, (2016).

26 Ricklefs, R. E. Cladogenesis and morphological diversification in passerine birds. *Nature* **430**, 338-341, (2004).

27 Title, P. O. & Burns, K. J. Rates of climatic niche evolution are correlated with species richness in a large and ecologically diverse radiation of songbirds. *Ecol. Lett.* **18**, 433-440, (2015).

28 Cooney, C. R., Seddon, N. & Tobias, J. A. Widespread correlations between climatic niche evolution and species diversification in birds. *J. Anim. Ecol.* **85**, 869-878, (2016).

29 Cardoso, G. C. & Mota, P. G. Speciational evolution of coloration in the genus *Carduelis*. *Evolution* **62**, 753-762, (2008).

30 Mason, N. A. *et al.* Song evolution, speciation, and vocal learning in passerine birds. *Evolution* **71**, 786-796, (2017).

31 Igea, J., Miller, E. F., Papadopulos, A. S. T. & Tanentzap, A. J. Seed size and its rate of evolution correlate with species diversification across angiosperms. *PLoS Biol.* **15**, e2002792, (2017).

32 Puttick, M. N., Clark, J. & Donoghue, P. C. J. Size is not everything: rates of genome size evolution, not C-value, correlate with speciation in angiosperms. *Proc. R. Soc. London Ser. B* **282**, 20152289, (2015).

33 Cantalapiedra, J. L., Prado, J. L., Hernandez Fernández, M. & Alberdi, M. T. Decoupled ecomorphological evolution and diversification in Neogene-Quaternary horses. *Science* **355**, 627-630, (2017).

34 Lee, M. S. Y., Sanders, K. L., King, B. & Palci, A. Diversification rates and phenotypic evolution in venomous snakes (Elapidae). *Royal Society Open Science* **3**, 150277, (2016).

35 Monroe, Melanie J. & Bokma, F. Do speciation rates drive rates of body size evolution in mammals? *Am. Nat.* **174**, 912-918, (2009).

36 Crouch, N. M. A. & Ricklefs, R. E. Speciation rate is independent of the rate of evolution of morphological size, shape, and absolute morphological specialization in a large clade of birds. *Am. Nat.* **193**, E78-E91, (2019).

37 Cooper, N., Thomas, G. H., Venditti, C., Meade, A. & Freckleton, R. P. A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biol. J. Linn. Soc.* **118**, 64-77, (2016).

38 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. B. & Salamin, N. Measurement errors should always be incorporated in phylogenetic comparative analysis. *Methods in Ecology and Evolution* **6**, 340-346, (2015).

39 Ho, L. S. T. & Ané, C. Intrinsic inference difficulties for trait evolution with Ornstein-Uhlenbeck models. *Methods in Ecology and Evolution* **5**, 1133-1146, (2014).

40 Pennell, M. W., Harmon, L. J. & Uyeda, J. C. Is there room for punctuated equilibrium in macroevolution? *Trends Ecol. Evol.* **25**, 23-32, (2014).

41 Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PloS one* **9**, e89543, (2014).

42 Elliot, M. G. & Mooers, A. Ø. Inferring ancestral states without assuming neutrality or gradualism using a stable model of continuous character evolution. *BMC Evol. Biol.* **14**, 226, (2014).

43 Smaers, J. B., Mongle, C. S. & Kandler, A. A multiple variance Brownian motion framework for estimating variable rates and inferring ancestral states. *Biol. J. Linn. Soc.* **118**, 78-94, (2016).

44 Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877-884, (1999).

45 Rabosky, D. L. Positive correlation between diversification rates and phenotypic evolvability can mimic punctuated equilibrium on molecular phylogenies. *Evolution* **66**, 2622-2627, (2012).

46 Simpson, E. H. The interpretation of interaction in contingency tables. *Journal of the Royal Statistical Society B* **13**, 238-241, (1951).

47 Pearl, J. Comment: Understanding Simpson's paradox. *American Statistician* **68**, 8-13, (2014).

48 Romanuk, T. N., Hayward, A. & Hutchings, J. A. Trophic level scales positively with body size in fishes. *Global Ecol. Biogeogr.* **20**, 231-240, (2011).

49 Steele, S. E. & López-Fernández, H. Body size diversity and frequency distributions of Neotropical cichlid fishes (Cichliformes: Cichlidae: Cichlinae). *PloS one* **9**, e106336, (2014).

50 Murillo-García, O. & De la vega, M. Divergence, convergence and phenotypic diversity of neotropical frugivorous bats. *Diversity* **10**, 100, (2018).

51 Morales, A. E., Ruedi, M., Field, K. & Carstens, B. C. Diversification rates have no effect on the convergent evolution of foraging strategies in the most speciose genus of bats, *Myotis*. *Evolution* **73**, 2263-2280, (2019).

52 Rodríguez-Robles, J. A. Molecular systematics of New World lampropeltinine snakes (Colubridae): implications for biogeography and evolution of food habits. *Biol. J. Linn. Soc.* **68**, 355-385, (1999).

53 Weir, J. T. & Mursleen, S. Diversity-dependent cladogenesis and trait evolution in the adaptive radiation of the auks (Aves: Alcidae). *Evolution* **67**, 403-416, (2013).

54 Moen, D. S., Irschick, D. J. & Wiens, J. J. Evolutionary conservatism and convergence both lead to striking similarity in ecology, morphology and performance across continents in frogs. *Proc. R. Soc. London Ser. B* **280**, 20132156, (2013).

55 Ahmadzadeh, F. *et al.* Cryptic speciation patterns in Iranian rock lizards uncovered by integrative taxonomy. *PloS one* **8**, e80563, (2013).

56 Gabirot, M., Lopez, P. & Martin, J. Differences in chemical sexual signals may promote reproductive isolation and cryptic speciation between Iberian wall lizard populations. *International journal of evolutionary biology* **2012**, 698520, (2012).

57 Hipsley, C. A., Miles, D. B. & Müller, J. Morphological disparity opposes latitudinal diversity gradient in lacertid lizards. *Biol. Lett.* **10**, 20140101, (2014).

58 Louca, S. & Pennell, M. W. Extant timetrees are consistent with a myriad of diversification histories. *Nature* **580**, 502-505, (2020).

59 Liow, L. H., Quental, T. B. & Marshall, C. R. When can decreasing diversification rates be detected with molecular phylogenies and the fossil record? *Syst. Biol.* **59**, 646-659, (2010).

60 Brown, J. H. *Macroecology*. (University of Chicago Press, 1995).

61 Schluter, D. Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372-380, (2001).

62 Arnegard, M. E. *et al.* Sexual signal evolution outpaces ecological divergence during electric fish species radiation. *Am. Nat.* **176**, 335-356, (2010).

63 Cooney, C. R. *et al.* Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature communications* **10**, 1773, (2019).

64 Rabosky, D. L. Reproductive isolation and the causes of speciation rate variation in nature. *Biol. J. Linn. Soc.* **118**, 13-25, (2016).

65 Henao Diaz, L. F., Harmon, L. J., Sugawara, M. T. C., Miller, E. T. & Pennell, M. W. Macroevolutionary diversification rates show time dependency. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 7403-7408, (2019).

66 Shafir, A., Azouri, D., Goldberg, E. E. & Mayrose, I. Heterogeneity in the rate of molecular sequence evolution substantially impacts the accuracy of detecting shifts in diversification rates. *Evolution* **74**, 1620-1639, (2020).

67 Losos, J. B. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.* **175**, 623-639, (2010).

68 Price, T. Sexual selection and natural selection in bird speciation. *Philos. Trans. R. Soc. London Ser. B* **353**, 251-260, (1998).

69 Salisbury, C. L., Seddon, N., Cooney, C. R. & Tobias, J. A. The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecol. Lett.* **15**, 847-855, (2012).

70 Moyle, R. G., Filardi, C. E., Smith, C. E. & Diamond, J. Explosive Pleistocene diversification and hemispheric expansion of a "great speciator". *Proc. Natl. Acad. Sci. U.S.A.* **106**, 1863-1868, (2009).

71 Title, P. O. & Rabosky, D. L. Tip rates, phylogenies and diversification: what are we estimating, and how good are the estimates? *Methods in Ecology and Evolution* **10**, 821-834, (2019).

72 Freckleton, R. P., Phillimore, A. B. & Pagel, M. Relating traits to diversification: a simple test. *Am. Nat.* **172**, 102-115, (2008).

73 Maliet, O., Hartig, F. & Morlon, H. A model with many small shifts for estimating species-specific diversification rates. *Nature Ecology & Evolution* **3**, 1086-1092, (2019).

74 Rabosky, D. L. *et al.* BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution* **5**, 701-707, (2014).

75 Chira, A. M. & Thomas, G. H. The impact of rate heterogeneity on inference of phylogenetic models of trait evolution. *J. Evol. Biol.* **29**, 2502-2518, (2016).

76 Zelditch, M. L., Ye, J., Mitchell, J. S. & Swiderski, D. L. Rare ecomorphological convergence on a complex adaptive landscape: body size and diet mediate evolution of jaw shape in squirrels (Sciuridae). *Evolution* **71**, 633-649, (2017).

77 Pimiento, C., Cantalapiedra, J. L., Shimada, K., Field, D. J. & Smaers, J. B. Evolutionary pathways toward gigantism in sharks and rays. *Evolution* **73**, 588-599, (2019).

78 Gómez-Robles, A., Smaers, J. B., Holloway, R. L., Polly, P. D. & Wood, B. A. Brain enlargement and dental reduction were not linked in hominin evolution. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 468-473, (2017).

79 Chira, A. M. *et al.* Correlates of rate heterogeneity in avian ecomorphological traits. *Ecol. Lett.* **21**, 1505-1514, (2018).

80 Morlon, H. *et al.* RPANDA: an R package for macroevolutionary analyses on phylogenetic trees. *Methods in Ecology and Evolution* **7**, 589-597, (2016).

81 Pennell, M. W., FitzJohn, R. G., Cornwell, W. K. & Harmon, L. J. Model adequacy and the macroevolution of angiosperm functional traits. *Am. Nat.* **186**, E33-E50, (2015).

82 Ho, L. S. T. & Ané, C. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.* **63**, 397-408, (2014).

83 Harvey, M. G. & Rabosky, D. L. Continuous traits and speciation rates: alternatives to state-dependent diversification models. *Methods in Ecology and Evolution* **9**, 984-993, (2018).

84 Rabosky, D. L. No substitute for real data: a cautionary note on the use of phylogenies from birth-death polytomy resolvers for downstream comparative analyses. *Evolution* **69**, 3207-3216, (2015).

85 Jetz, W. & Pyron, R. A. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat Ecol Evol* **2**, 850-858, (2018).

86 Faurby, S. *et al.* PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. *Ecology* **99**, 2626, (2018).

87 Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W. & Pyron, R. A. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol. Conserv.* **204**, 23-31, (2016).

88 Schliep, K. P. phangorn: phylogenetic analysis in R. *Bioinformatics* **27**, 592-593, (2011).

89 Wilman, H. *et al.* EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027, (2014).

90 Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C. & Costa, G. C. AmphiBIO, a global database for amphibian ecological traits. *Scientific Data* **4**, 170123, (2017).

91 Amado, T. F., Bidau, C. J. & Olalla-Tárraga, M. Á. Geographic variation of body size in New World anurans: energy and water in a balance. *Ecography* **42**, 456-466, (2018).

92 Froese, R. & Pauly, D. www.fishbase.org (accessed 27/02/2019).

93 Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I. & Meiri, S. Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecol. Biogeogr.* **25**, 187-197, (2016).

94 Hadfield, J. D. MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22, (2010).

FIGURE LEGENDS

Figure 1. **Comparison of the performance of different approaches for testing correlations between rates of speciation and trait evolution.** Results are based on simulated datasets of 250-tip trees (*n* = 100) assuming strong correlations between rates (columns 1 and 2), with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}). See *Methods* for details of the simulation procedure, rate metrics and significance tests used. The grey shaded area indicates false discovery (Type I error) rates of <5%.

Figure 2. **The Correlated Speciation and Trait Rates Simulation (Cor-STRATES) framework.** This schematic provides an overview of the steps involved in the best-performing approach investigated in this study for testing relationships between rates of speciation and trait evolution using phylogenetic data. See text for full details.

Figure 3. **Phylogenetic patterns of evolutionary rate heterogeneity for five vertebrate clades.** For each group, mean per-branch rates of speciation (λ_{BAMM}, left) and body size evolution (σ^2_{BT}, right) are shown. Dark colours correspond to slow rates, light colours correspond to fast rates.

Figure 4. **The relationship between rates of speciation and body size evolution for five vertebrate groups. a-e,** Scatterplots (left column) show the relationship between log-transformed tip rates of speciation (λ_{BAMM}) and body size evolution (σ^2_{BT}) in each group. Histograms (right column) show the correlation coefficient for the observed relationship (arrow) in relation to a null distribution of correlation coefficients calculated from 200 simulated datasets. NB: outlier points (*n* = 6) with extremely small relative trait rate values have been omitted from the scatterplot in **c**. The trend lines for the scatterplots are based on ordinary least-squares regression and are indicative only.

Figure 5. **Heterogeneity in the relationship between rates of speciation and body size evolution among major vertebrate subclades.** Plot shows the distribution of mean effect sizes (points) and 95% confidence intervals (lines) for the relationship between rates of speciation (λ_{BAMM}) and body size evolution (σ^2_{BT}) within subclades of five vertebrate groups. Tests were performed using rate comparisons among tips only or across all branches in the tree. Filled points indicate cases in which the relationship between rates is statistically significant ($P < 0.05$) based on comparisons to simulated datasets (*n* = 200). Figures in parentheses following clade names indicate taxonomic species richness and the proportion of those taxa included in the trait rates analysis. Asterisks indicate clades exhibiting significant associations in either or both analyses.

Extended Data Figure 1. **The performance of different phylogenetic approaches for estimating rates of speciation (λ) and trait evolution (σ^2).** Plots show the error, bias and correlation of estimated rates of speciation (**c**) and trait evolution (**b**-**c**) compared to true (i.e. simulated) values. In **b**, results are based on comparing rates across all branches of the tree, whereas in **c**, results are based on comparing tip rates only. Results are based on fitting models to 100 simulated tree and trait datasets, each with 250 tips. Boxplots show the median value (thick line) and 0.25-0.75 (box) and 0.05-0.95 (whiskers) quantile ranges. BT, BayesTraits; ST, StableTraits.

Extended Data Figure 2. **Comparison of the performance of different approaches for testing correlations between rates of speciation and trait evolution.** Results are based on simulated datasets of 250-tip trees (*n* = 100) assuming strong correlations between rates (columns 1 and 2), with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates also estimated using BAMM (σ^2_{BAMM}). See *Methods* for details of the simulation procedure, rate metrics and significance tests used. The grey shaded area indicates false discovery (Type I error) rates of <5%.

Extended Data Figure 3. **Comparison of mean standardised effect sizes derived from the 'simulation + rescale' approach using alternate rate metrics.** Speciation rates are estimated using BAMM (λ_{BAMM}) and trait rates are estimated using either BayesTraits (σ^2_{BT}) or BAMM (σ^2_{BAMM})**.** Results are based on applying the 'tree-transformation + simulation' method to datasets of 250-tip trees (*n* = 100) generated assuming strong correlations between rates (columns 1 and 2).

Extended Data Figure 4. **Comparison of the performance of the 'simulation + rescale' approach with varying tree size and simulated correlation strength.** Results are based on simulated datasets of 100 trees, with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}). For the scenarios involving correlated rates, solid and dashed lines correspond to strong ($r = \pm 1$) and weaker ($r = \pm 0.5$) simulated correlation strengths, respectively. (Note: realised correlation strengths associated with these scenarios are lower than implied by the generating values; see Extended Data Figure 10). The grey shaded area indicates false discovery (Type I error) rates of <5%. ME, measurement error.

Extended Data Figure 5. **Comparison of the performance of the 'simulation + rescale' approach with decreasing sampling proportions.** Results are based on simulated datasets of 250-tip trees (*n* = 100) assuming strong correlations between rates (columns 1 and 2), with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}). The grey shaded area indicates false discovery (Type I error) rates of <5%. ME, measurement error.

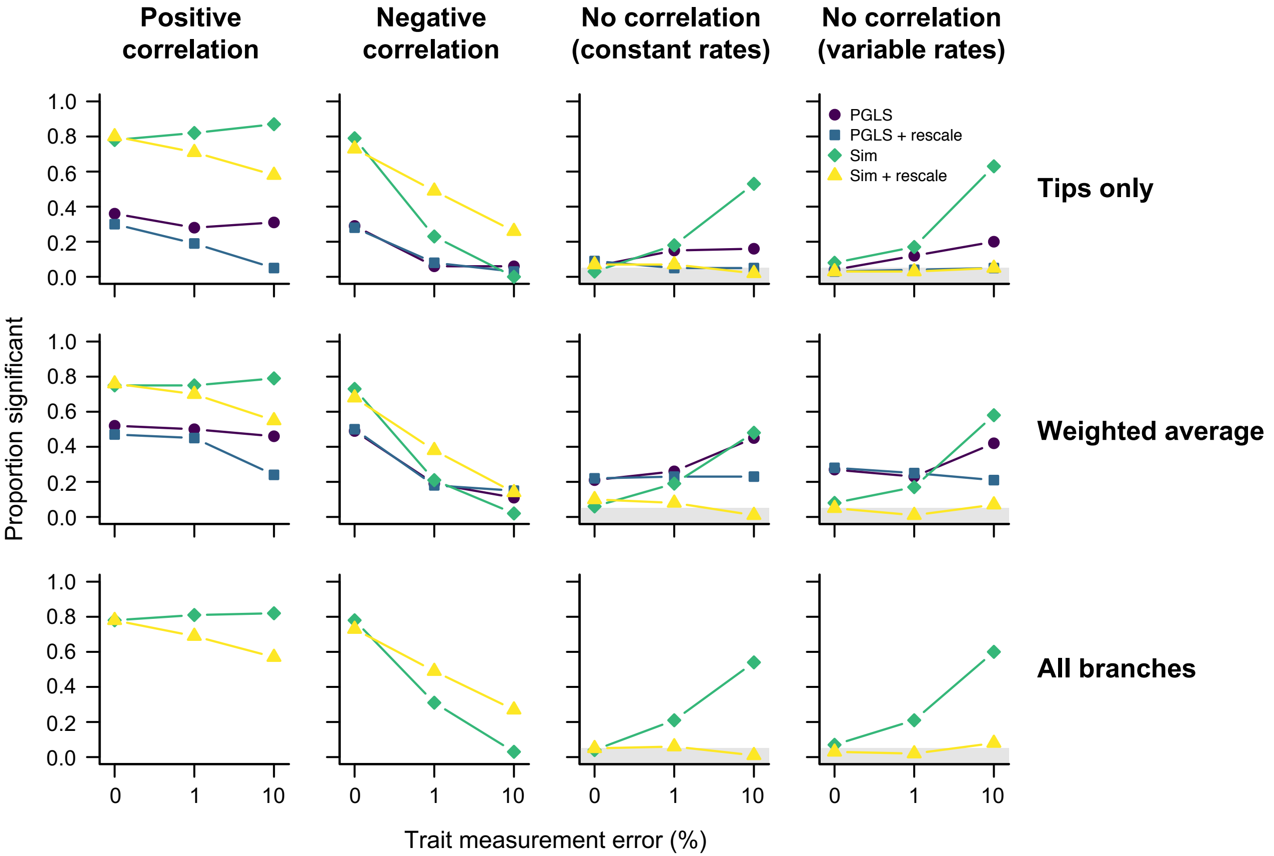
Extended Data Figure 6. **Comparison of the performance of the 'simulation + rescale' approach with increasing relative extinction (turnover) rates.** Results are based on simulated datasets of 250-tip trees (n = 100) assuming strong correlations between rates (columns 1 and 2), with speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}). The grey shaded area indicates false discovery (Type I error) rates of <5%. ME, measurement error.

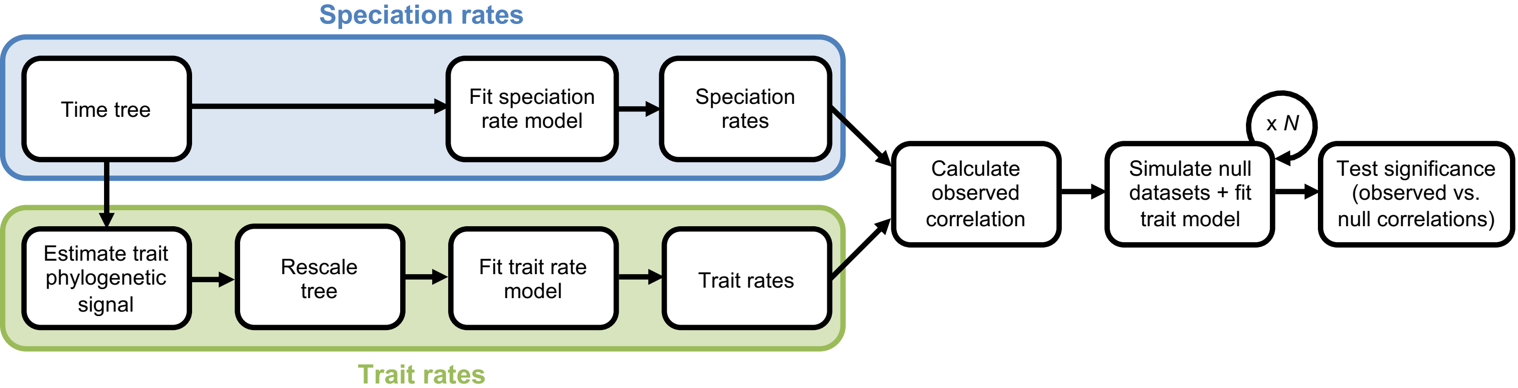
Extended Data Figure 7. **Results for tests of the relationship between rates of speciation and body size evolution within five vertebrate taxa.** Results are based on speciation rates estimated using BAMM (λ_{BAMM}) and body size rates estimated using BayesTraits (σ^2_{BT}). N = total species richness; N_{samp} = number of species sampled in rate analyses; phy. sig. = body size phylogenetic signal (Pagel's lambda); ρ_{obs} = observed correlation coefficient (Spearman's ρ); ρ_{null} = null correlation coefficients derived from null simulations (n = 200); SES = standardised effect size.

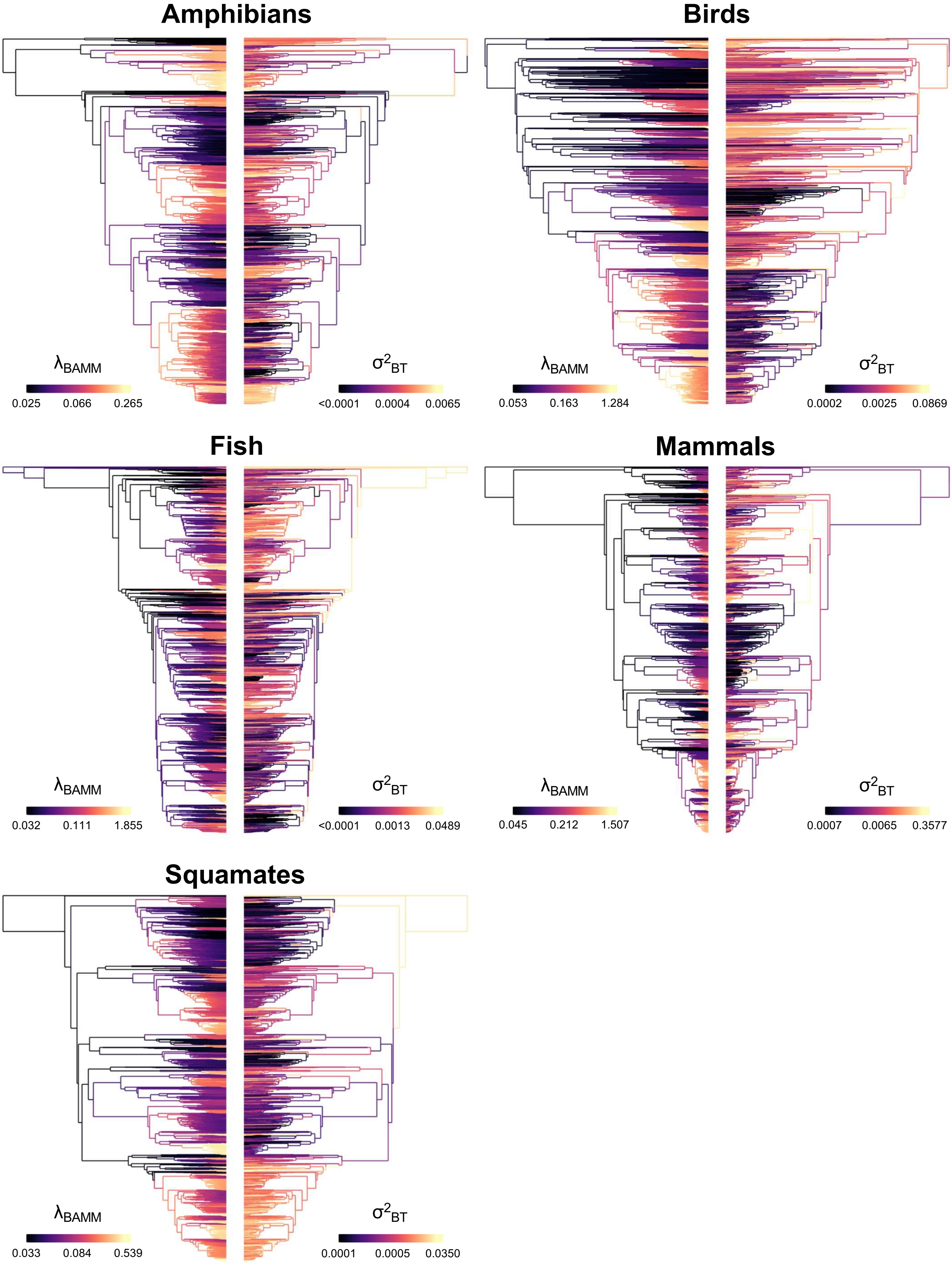
Extended Data Figure 8. **Relationships between rates of speciation and body size evolution in vertebrate subclades.** Plots show the relationship between log-transformed tip rates of speciation (λ_{BAMM}) and body size evolution (σ^2_{BT}) in each clade. Colours reflect the five vertebrate groups (birds = blue, mammals = red, amphibians = green, squamates = purple, fish = orange). Inset numbers give the mean effect size for each relationship, with significant ($P < 0.05$) associations marked with an asterisk and highlighted in bold.

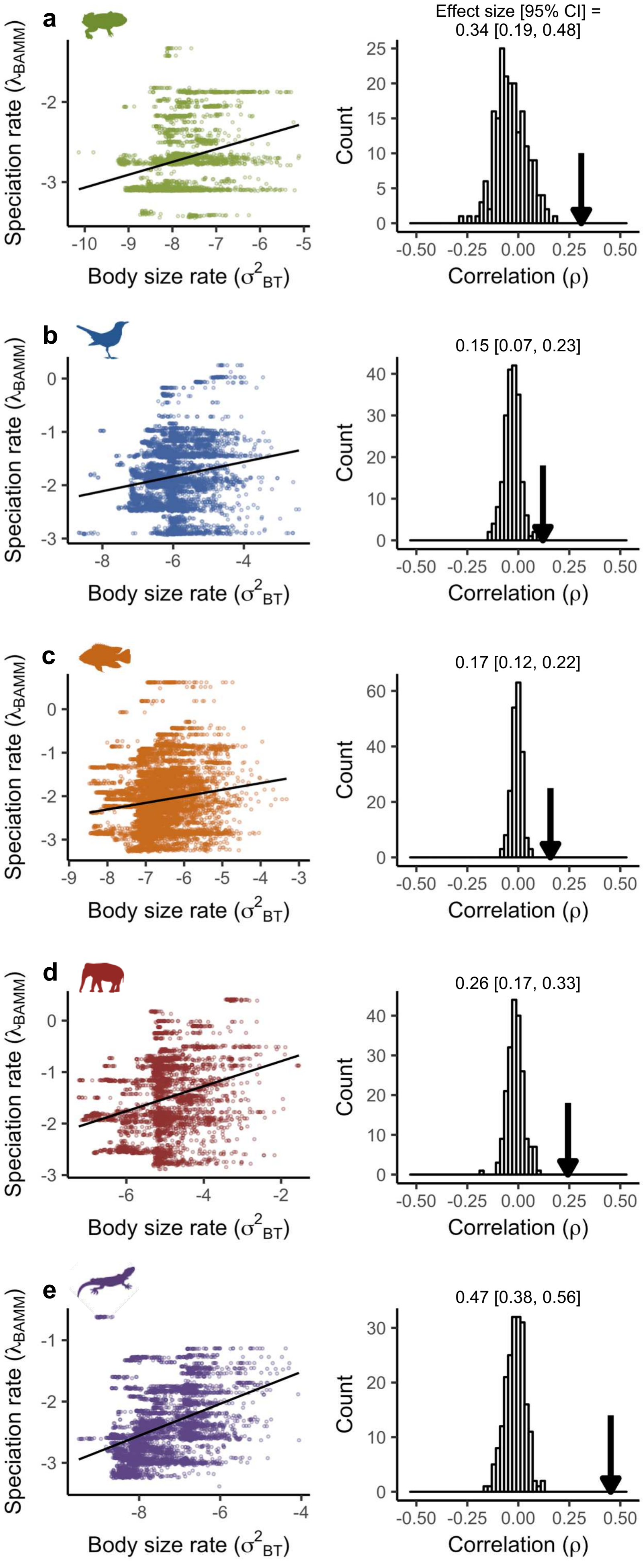
Extended Data Figure 9. **Multipredictor models of effect sizes measuring the strength of the association between rates of speciation and body size evolution in vertebrate subclades.** Results are based on speciation rates estimated using BAMM (λ_{BAMM}) and trait rates estimated using BayesTraits (σ^2_{BT}). All predictor variables were standardised (mean = 0, sd = 1) prior to analysis. SE = standard error. *, $P_{MCMC} < 0.05$.

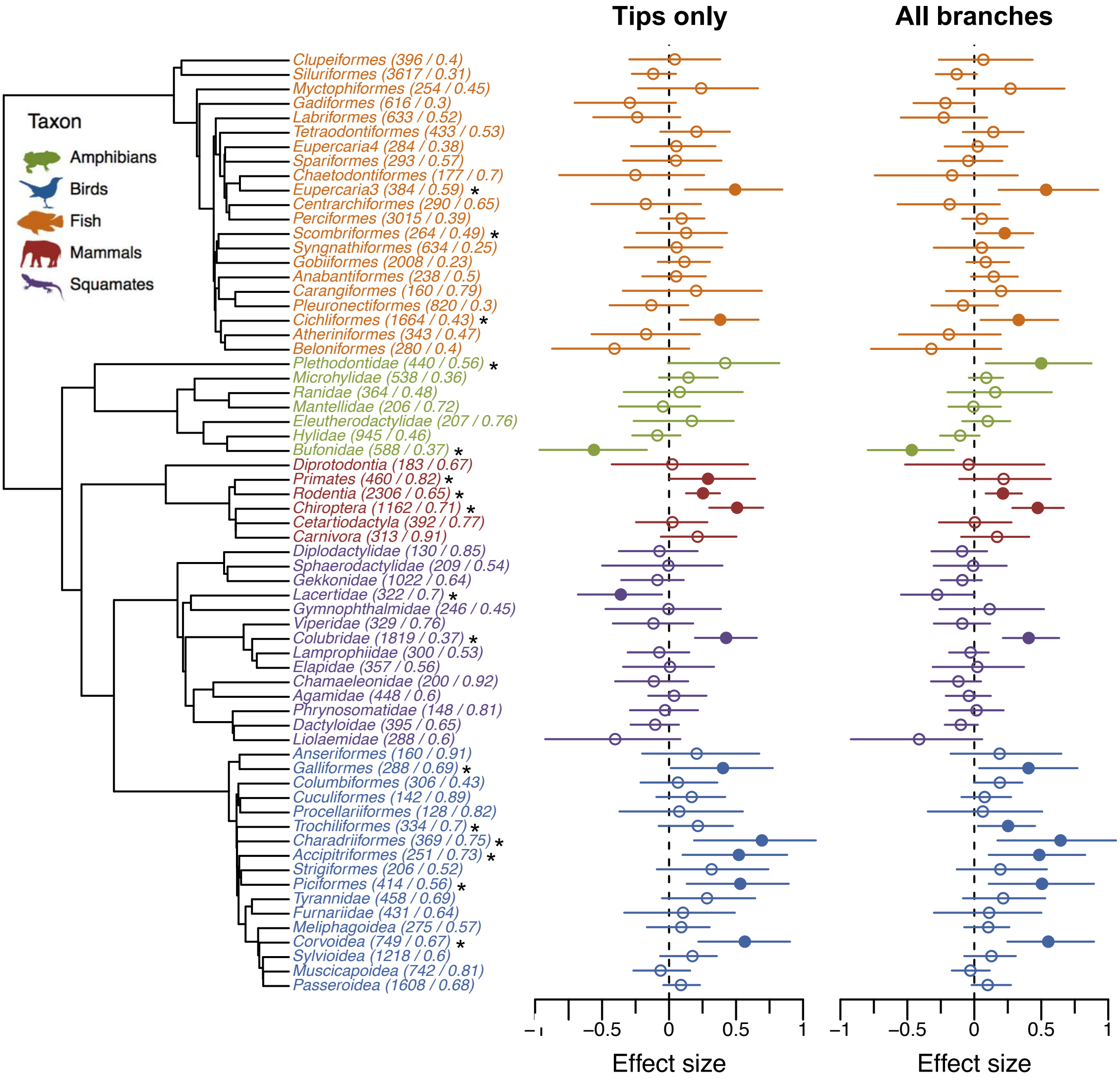
Extended Data Figure 10. **Mean (sd) correlation coefficients (Pearson's *r*) for the realised relationship between simulated rates of speciation and trait evolution.** Realised rates of trait evolution are inferred by calculating the squared-trait distance between known simulated ancestral and descendent nodes in the tree, divided by phylogenetic branch length (i.e. time). Note: Pearson's r values in the table header refer to the correlation strength between speciation and trait rates used in the stochastic model used to generate trait values. n = 100 trees in each case.

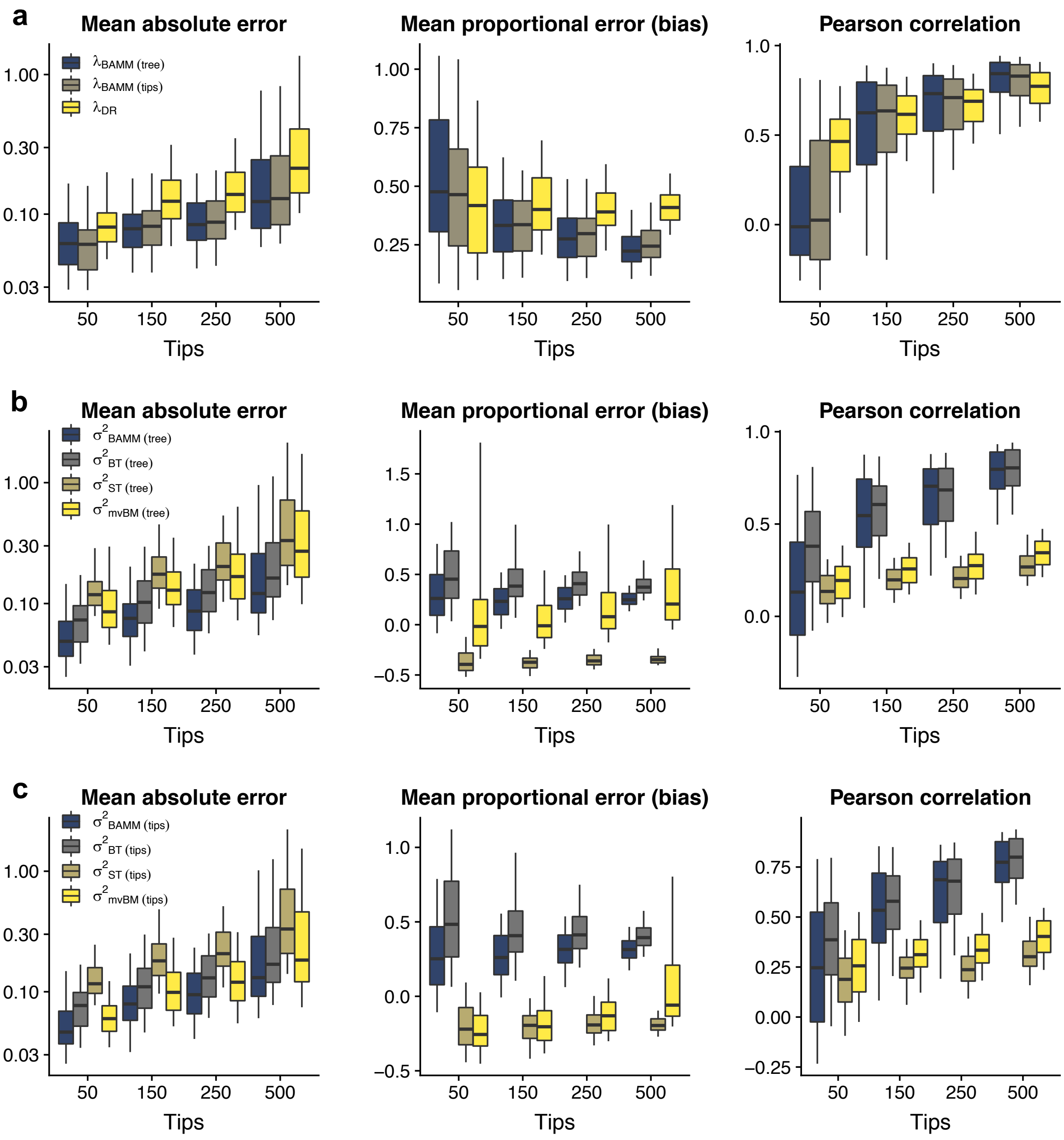

Positive correlation
Negative correlation
No correlation (constant rates)
No correlation (variable rates)
PGLS
PGLS + rescale
Sim
Sim + rescale
Tips only
Weighted average
All branches
Proportion significant
0.0
0.2
0.4
0.6
0.8
1.0
0
1
10
Trait measurement error (%)

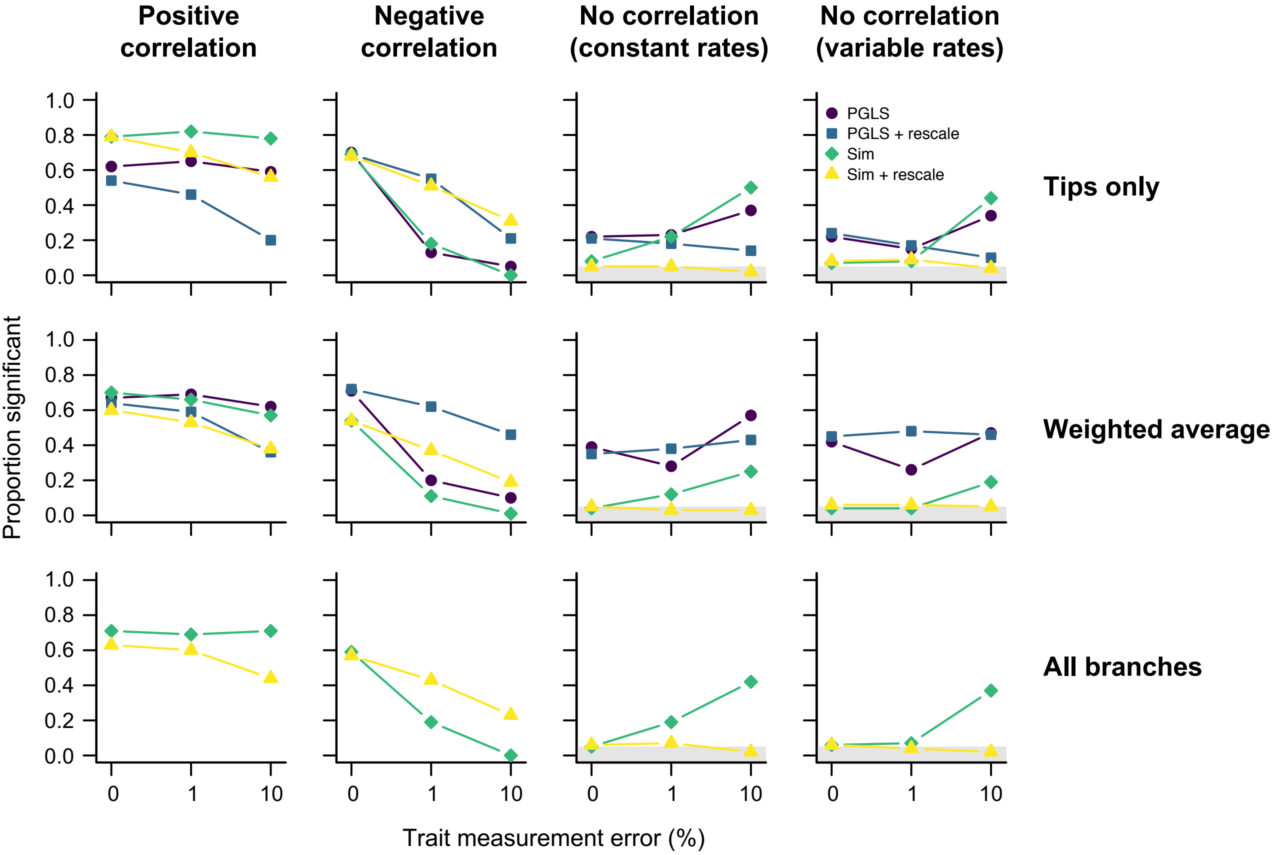

Speciation rates
Time tree
Fit speciation rate model
Speciation rates
Estimate trait phylogenetic signal
Rescale tree
Fit trait rate model
Trait rates
Trait rates
Calculate observed correlation
Simulate null datasets + fit trait model
x *N*
Test significance (observed vs. null correlations)

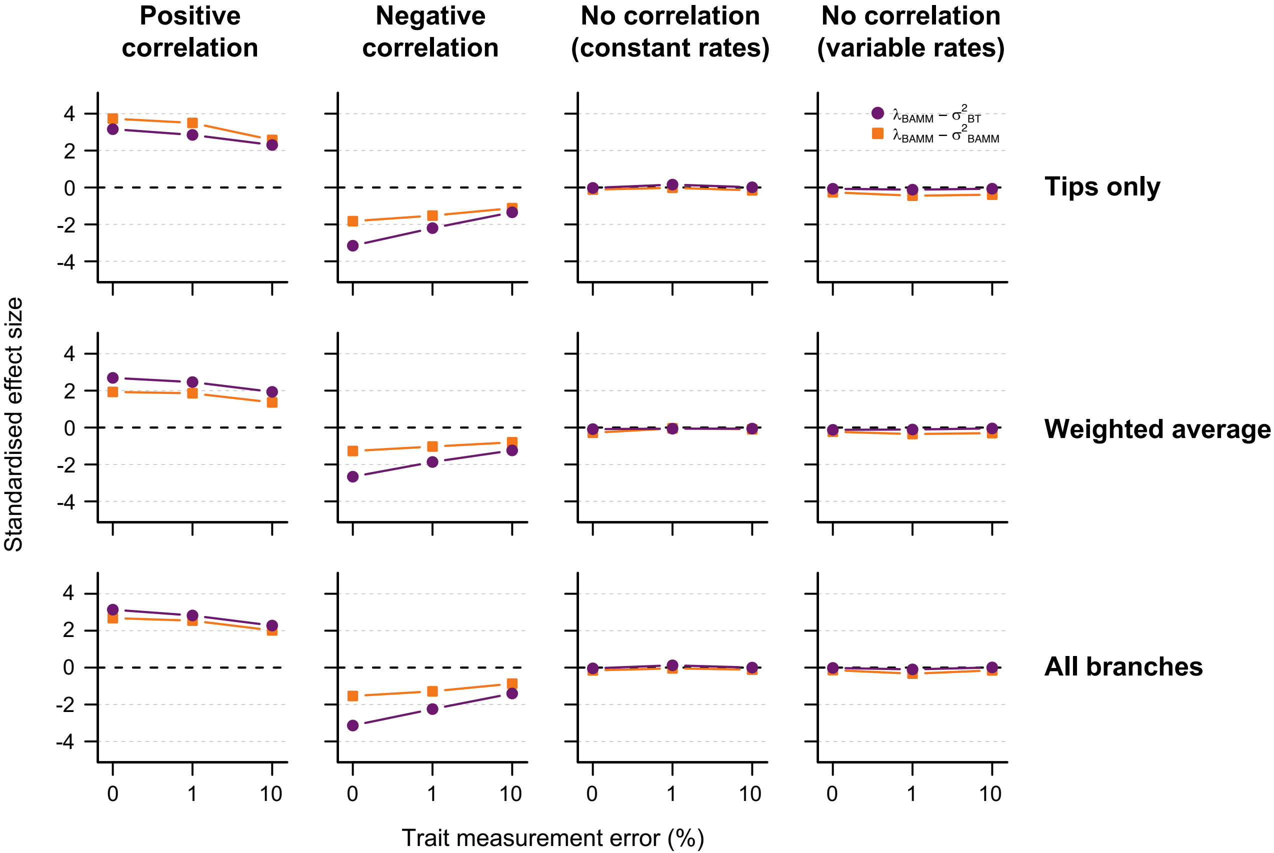

Amphibians
λBAMM
0.025
0.066
0.265
σ2BT
<0.0001
0.0004
0.0065
Birds
λBAMM
0.053
0.163
1.284
σ2BT
0.0002
0.0025
0.0869
Fish
λBAMM
0.032
0.111
1.855
σ2BT
<0.0001
0.0013
0.0489
Mammals
λBAMM
0.045
0.212
1.507
σ2BT
0.0007
0.0065
0.3577
Squamates
λBAMM
0.033
0.084
0.539
σ2BT
0.0001
0.0005
0.0350

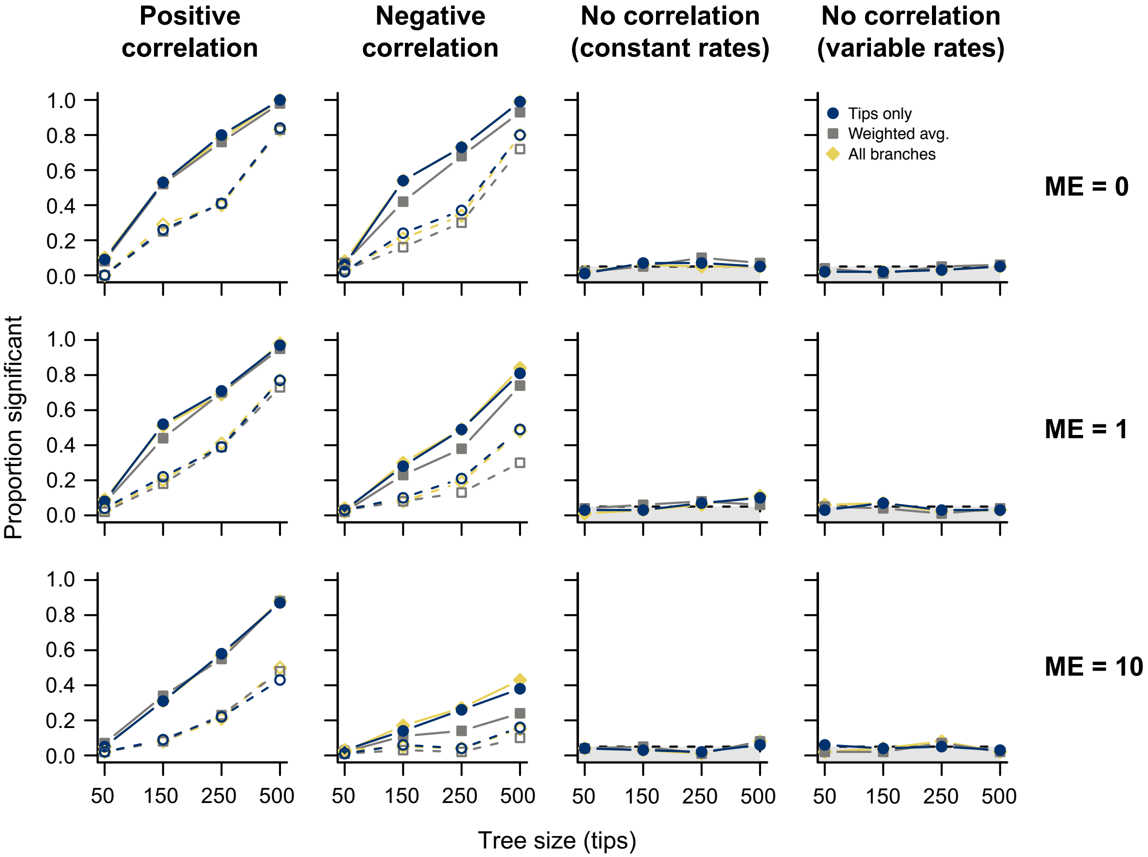

a
Effect size [95% CI] =
0.34 [0.19, 0.48]
Speciation rate (λ_{BAMM})
-2
-3
-10
-9
-8
-7
-6
-5
Body size rate (σ^2_{BT})
Count
25
20
15
10
5
0
-0.50
-0.25
0.00
0.25
0.50
Correlation (ρ)
b
0.15 [0.07, 0.23]
Speciation rate (λ_{BAMM})
0
-1
-2
-3
-8
-6
-4
Body size rate (σ^2_{BT})
Count
40
30
20
10
0
-0.50
-0.25
0.00
0.25
0.50
Correlation (ρ)
c
0.17 [0.12, 0.22]
Speciation rate (λ_{BAMM})
0
-1
-2
-3
-9
-8
-7
-6
-5
-4
-3
Body size rate (σ^2_{BT})
Count
60
40
20
0
-0.50
-0.25
0.00
0.25
0.50
Correlation (ρ)
d
0.26 [0.17, 0.33]
Speciation rate (λ_{BAMM})
0
-1
-2
-3
-6
-4
-2
Body size rate (σ^2_{BT})
Count
40
30
20
10
0
-0.50
-0.25
0.00
0.25
0.50
Correlation (ρ)
e
0.47 [0.38, 0.56]
Speciation rate (λ_{BAMM})
-1
-2
-3
-8
-6
-4
Body size rate (σ^2_{BT})
Count
30
20
10
0
-0.50
-0.25
0.00
0.25
0.50
Correlation (ρ)

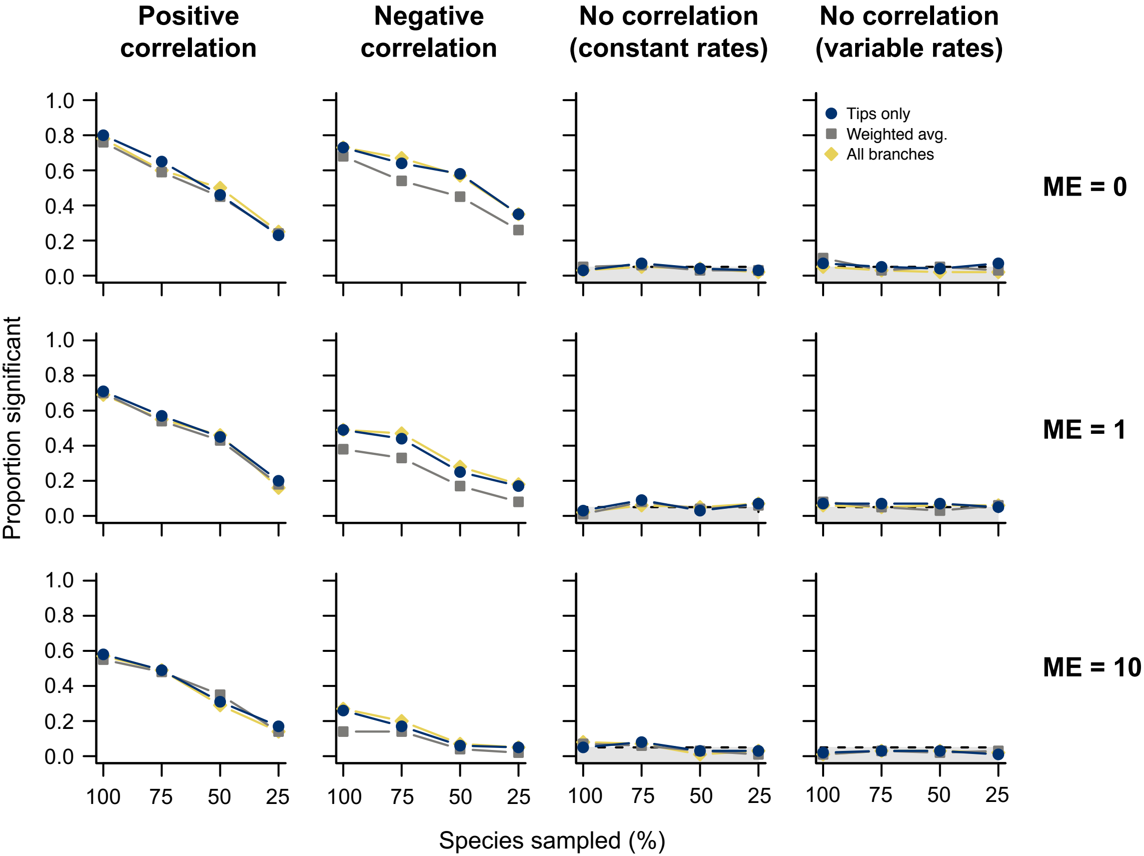

Tips only
All branches
Taxon
Amphibians
Birds
Fish
Mammals
Squamates
Clupeiformes (396 / 0.4)
Siluriformes (3617 / 0.31)
Myctophiformes (254 / 0.45)
Gadiformes (616 / 0.3)
Labriformes (633 / 0.52)
Tetraodontiformes (433 / 0.53)
Eupercaria4 (284 / 0.38)
Spariformes (293 / 0.57)
Chaetodontiformes (177 / 0.7)
Eupercaria3 (384 / 0.59) *
Centrarchiformes (290 / 0.65)
Perciformes (3015 / 0.39)
Scombriformes (264 / 0.49) *
Syngnathiformes (634 / 0.25)
Gobiiformes (2008 / 0.23)
Anabantiformes (238 / 0.5)
Carangiformes (160 / 0.79)
Pleuronectiformes (820 / 0.3)
Cichliformes (1664 / 0.43) *
Atheriniformes (343 / 0.47)
Beloniformes (280 / 0.4)
Plethodontidae (440 / 0.56) *
Microhylidae (538 / 0.36)
Ranidae (364 / 0.48)
Mantellidae (206 / 0.72)
Eleutherodactylidae (207 / 0.76)
Hylidae (945 / 0.46)
Bufonidae (588 / 0.37) *
Diprotodontia (183 / 0.67)
Primates (460 / 0.82) *
Rodentia (2306 / 0.65) *
Chiroptera (1162 / 0.71) *
Cetartiodactyla (392 / 0.77)
Carnivora (313 / 0.91)
Diplodactylidae (130 / 0.85)
Sphaerodactylidae (209 / 0.54)
Gekkonidae (1022 / 0.64)
Lacertidae (322 / 0.7) *
Gymnophthalmidae (246 / 0.45)
Viperidae (329 / 0.76)
Colubridae (1819 / 0.37) *
Lamprophiidae (300 / 0.53)
Elapidae (357 / 0.56)
Chamaeleonidae (200 / 0.92)
Agamidae (448 / 0.6)
Phrynosomatidae (148 / 0.81)
Dactyloidae (395 / 0.65)
Liolaemidae (288 / 0.6)
Anseriformes (160 / 0.91)
Galliformes (288 / 0.69) *
Columbiformes (306 / 0.43)
Cuculiformes (142 / 0.89)
Procellariiformes (128 / 0.82)
Trochiliformes (334 / 0.7) *
Charadriiformes (369 / 0.75) *
Accipitriformes (251 / 0.73) *
Strigiformes (206 / 0.52)
Piciformes (414 / 0.56) *
Tyrannidae (458 / 0.69)
Furnariidae (431 / 0.64)
Meliphagoidea (275 / 0.57)
Corvoidea (749 / 0.67) *
Sylvioidea (1218 / 0.6)
Muscicapoidea (742 / 0.81)
Passeroidea (1608 / 0.68)
–1
–0.5
0
0.5
1
Effect size
–1
–0.5
0
0.5
1
Effect size

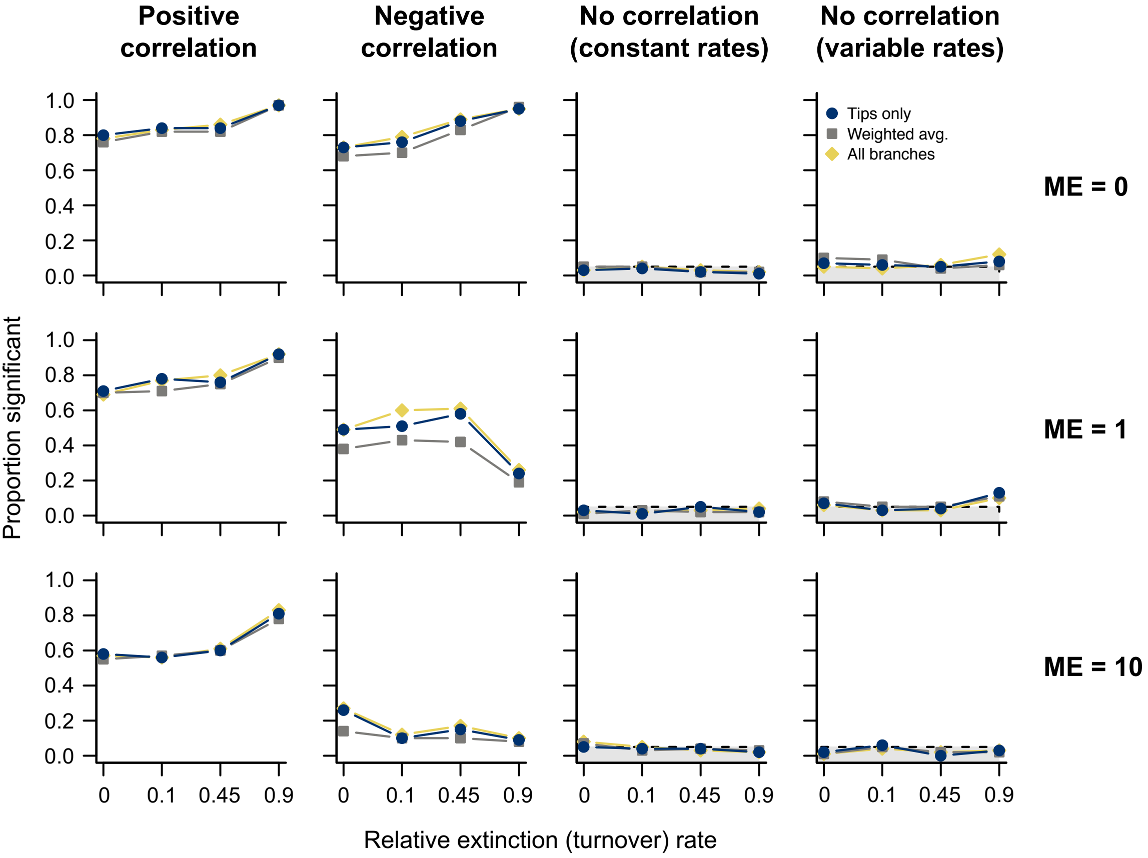

a
Mean absolute error
λ_{BAMM} (tree)
λ_{BAMM} (tips)
λ_{DR}
1.00
0.30
0.10
0.03
50
150
250
500
Tips
Mean proportional error (bias)
1.00
0.75
0.50
0.25
50
150
250
500
Tips
Pearson correlation
1.0
0.5
0.0
50
150
250
500
Tips
b
Mean absolute error
σ^2_{BAMM} (tree)
σ^2_{BT} (tree)
σ^2_{ST} (tree)
σ^2_{mvBM} (tree)
1.00
0.30
0.10
0.03
50
150
250
500
Tips
Mean proportional error (bias)
1.5
1.0
0.5
0.0
−0.5
50
150
250
500
Tips
Pearson correlation
1.0
0.5
0.0
50
150
250
500
Tips
c
Mean absolute error
σ^2_{BAMM} (tips)
σ^2_{BT} (tips)
σ^2_{ST} (tips)
σ^2_{mvBM} (tips)
1.00
0.30
0.10
0.03
50
150
250
500
Tips
Mean proportional error (bias)
1.0
0.5
0.0
−0.5
50
150
250
500
Tips
Pearson correlation
0.75
0.50
0.25
0.00
−0.25
50
150
250
500
Tips


Positive correlation
Negative correlation
No correlation (constant rates)
No correlation (variable rates)
Tips only
Weighted average
All branches
PGLS
PGLS + rescale
Sim
Sim + rescale
Proportion significant
1.0
0.8
0.6
0.4
0.2
0.0
0
1
10
Trait measurement error (%)

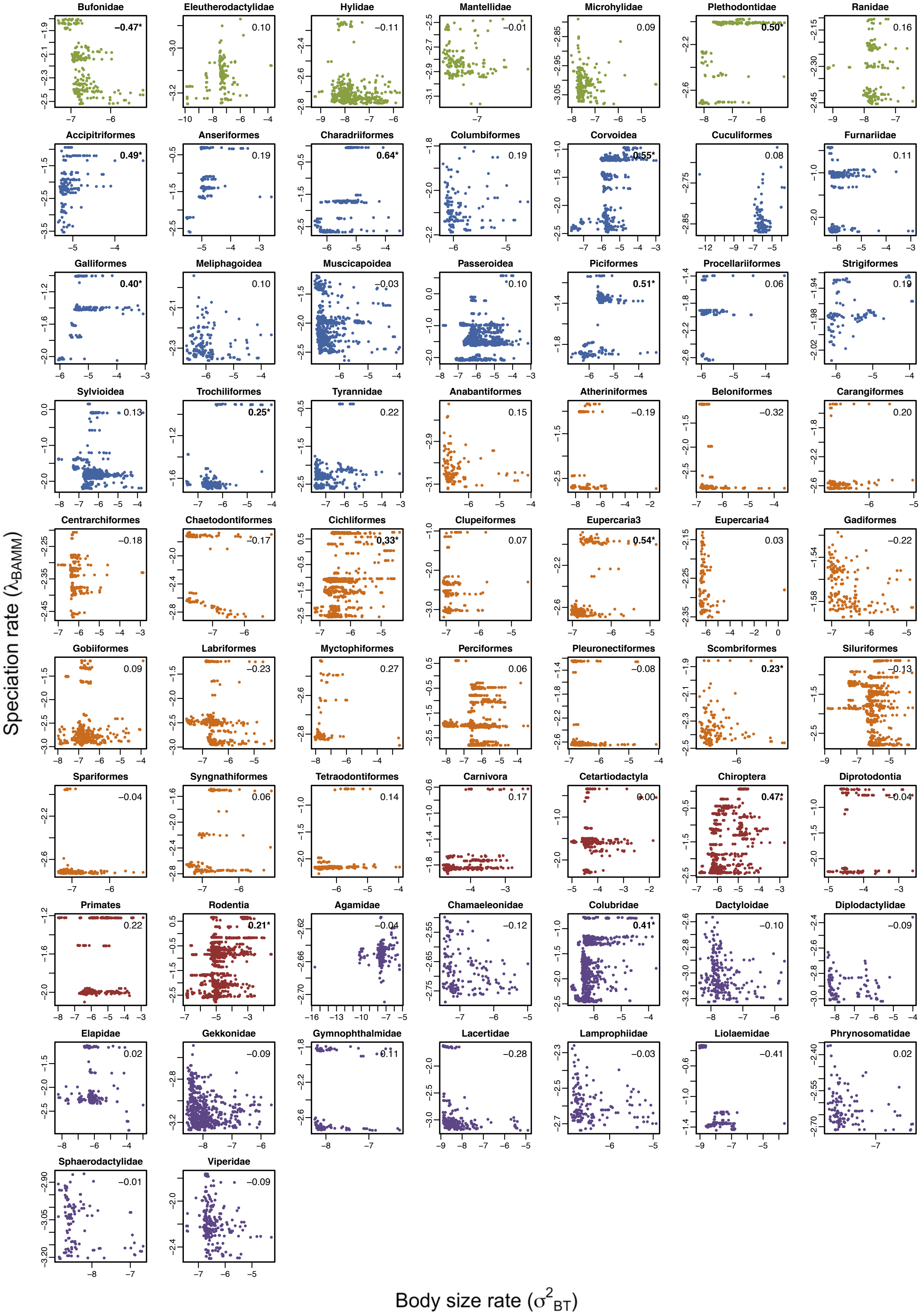

Positive correlation
Negative correlation
No correlation (constant rates)
No correlation (variable rates)
$\lambda_{BAMM} - \sigma^2_{BT}$
$\lambda_{BAMM} - \sigma^2_{BAMM}$
Tips only
Weighted average
All branches
Standardised effect size
4
2
0
-2
-4
0
1
10
Trait measurement error (%)


Positive correlation
Negative correlation
No correlation (constant rates)
No correlation (variable rates)
ME = 0
ME = 1
ME = 10
Tips only
Weighted avg.
All branches
Proportion significant
1.0
0.8
0.6
0.4
0.2
0.0
50
150
250
500
Tree size (tips)


Positive correlation
Negative correlation
No correlation (constant rates)
No correlation (variable rates)
Tips only
Weighted avg.
All branches
ME = 0
ME = 1
ME = 10
Proportion significant
1.0
0.8
0.6
0.4
0.2
0.0
100
75
50
25
Species sampled (%)


Positive correlation
Negative correlation
No correlation (constant rates)
No correlation (variable rates)
● Tips only
■ Weighted avg.
◆ All branches
ME = 0
ME = 1
ME = 10
Proportion significant
0.0
0.2
0.4
0.6
0.8
1.0
0
0.1
0.45
0.9
Relative extinction (turnover) rate

Taxon	N	N_{samp}	***Phy. sig.***	**Dataset**	ρ_{obs}	ρ_{null} **[95% CI]**	**Effect size [95% CI]**	**SES**	P
Amphibians	7238	3193	0.96	Tips only	0.309	-0.035 [-0.175, 0.119]	0.343 [0.190, 0.483]	4.515	<0.01
				All branches	0.301	-0.010 [-0.144, 0.133]	0.311 [0.168, 0.445]	4.198	<0.01
Birds	9993	6670	0.98	Tips only	0.120	-0.030 [-0.112, 0.047]	0.150 [0.074, 0.232]	3.826	0.02
				All branches	0.108	-0.005 [-0.092, 0.071]	0.113 [0.037, 0.200]	2.845	0.02
Fish	31516	10868	0.96	Tips only	0.157	-0.008 [-0.062, 0.041]	0.166 [0.116, 0.219]	6.553	<0.01
				All branches	0.171	0.022 [-0.027, 0.068]	0.148 [0.102, 0.198]	6.189	<0.01
Mammals	5561	4095	0.99	Tips only	0.243	-0.014 [-0.084, 0.077]	0.257 [0.166, 0.327]	6.306	<0.01
				All branches	0.253	0.029 [-0.037, 0.108]	0.224 [0.145, 0.291]	5.867	<0.01
Squamates	9755	5398	0.96	Tips only	0.453	-0.016 [-0.112, 0.068]	0.468 [0.384, 0.564]	9.758	<0.01
				All branches	0.453	0.007 [-0.098, 0.078]	0.447 [0.376, 0.552]	9.533	<0.01


Bufonidae
−0.47*
Eleutherodactylidae
0.10
Hylidae
−0.11
Mantellidae
−0.01
Microhylidae
0.09
Plethodontidae
0.50*
Ranidae
0.16
Accipitriformes
0.49*
Anseriformes
0.19
Charadriiformes
0.64*
Columbiformes
0.19
Corvoidea
0.55*
Cuculiformes
0.08
Furnariidae
0.11
Galliformes
0.40*
Meliphagoidea
0.10
Muscicapoidea
−0.03
Passeroidea
0.10
Piciformes
0.51*
Procellariiformes
0.06
Strigiformes
0.19
Sylvioidea
0.13
Trochiliformes
0.25*
Tyrannidae
0.22
Anabantiformes
0.15
Atheriniformes
−0.19
Beloniformes
−0.32
Carangiformes
0.20
Centrarchiformes
−0.18
Chaetodontiformes
−0.17
Cichliformes
0.33*
Clupeiformes
0.07
Eupercaria3
0.54*
Eupercaria4
0.03
Gadiformes
−0.22
Gobiiformes
0.09
Labriformes
−0.23
Myctophiformes
0.27
Perciformes
0.06
Pleuronectiformes
−0.08
Scombriformes
0.23*
Siluriformes
−0.13
Spariformes
−0.04
Syngnathiformes
0.06
Tetraodontiformes
0.14
Carnivora
0.17
Cetartiodactyla
0.00
Chiroptera
0.47*
Diprotodontia
−0.04
Primates
0.22
Rodentia
0.21*
Agamidae
−0.04
Chamaeleonidae
−0.12
Colubridae
0.41*
Dactyloidae
−0.10
Diplodactylidae
−0.09
Elapidae
0.02
Gekkonidae
−0.09
Gymnophthalmidae
0.11
Lacertidae
−0.28
Lamprophiidae
−0.03
Liolaemidae
−0.41
Phrynosomatidae
0.02
Sphaerodactylidae
−0.01
Viperidae
−0.09
Speciation rate (λ_{BAMM})
Body size rate (σ^2_{BT})

	Tips only		**All branches**	
Term	**Estimate [95% CI]**	**P_{MCMC}**	**Estimate [95% CI]**	**P_{MCMC}**
Effect size				
(Intercept)	0.109 [-1.378, 1.822]	0.590	0.182 [-1.386, 1.572]	0.562
Crown age	0.037 [-0.037, 0.114]	0.347	0.016 [-0.051, 0.094]	0.662
Clade richness	0.044 [-0.032, 0.119]	0.264	0.031 [-0.041, 0.104]	0.398
Sampling proportion	0.034 [-0.048, 0.123]	0.411	0.018 [-0.062, 0.097]	0.644
Trait phylogenetic signal	-0.047 [-0.113, 0.023]	0.164	-0.051 [-0115, 0.011]	0.116
Speciation rate variation	0.005 [-0.065, 0.071]	0.883	0.006 [-0.059, 0.069]	0.849
Body size rate variation	-0.014 [-0.076, 0.037]	0.631	-0.031 [-0.086, 0.026]	0.267
Absolute effect size				
(Intercept)	0.164 [-0.370, 0.697]	0.167	0.206 [-0.536, 0.748]	0.174
Crown age	0.000 [-0.052, 0.056]	0.996	-0.005 [-0.055, 0.049]	0.852
Clade richness	0.000 [-0.053, 0.057]	0.995	0.001 [-0.055, 0.056]	0.973
Sampling proportion	0.001 [-0.060, 0.060]	0.992	-0.007 [-0.067, 0.052]	0.834
Trait phylogenetic signal	0.003 [-0.048, 0.053]	0.916	-0.014 [-0.064, 0.032]	0.570
Speciation rate variation	0.059 [0.009, 0.111]	0.024*	0.042 [-0.005, 0.090]	0.084
Body size rate variation	0.000 [-0.043, 0.043]	0.989	-0.010 [-0.049, 0.032]	0.630
Standardised effect size				
(Intercept)	-0.736 [-8.420, 9.610]	0.515	2.908 [-7.752, 11.083]	0.508
Crown age	0.126 [-0.280, 0.563]	0.549	-0.020 [-0.491, 0.428]	0.946
Clade richness	0.372 [-0.062, 0.818]	0.097	0.235 [-0.214, 0.725]	0.319
Sampling proportion	0.151 [-0.306, 0.640]	0.532	-0.017 [-0.538, 0.482]	0.950
Trait phylogenetic signal	-0.195 [-0.579, 0.186]	0.327	-0.279 [-0.676, 0.159]	0.188
Speciation rate variation	0.110 [-0.268, 0.493]	0.577	0.089 [-0.309, 0.508]	0.656
Body size rate variation	-0.023 [-0.378, 0.291]	0.895	-0.144 [-0.488, 0.212]	0.419
Absolute standardised effect size				
(Intercept)	1.113 [-0.073, 2.720]	0.061	1.215 [-0.009, 2.822]	0.049*
Crown age	-0.048 [-0.328, 0.210]	0.734	-0.116 [-0.407, 0.163]	0.421
Clade richness	0.400 [0.114, 0.705]	0.010*	0.372 [0.056, 0.664]	0.016*
Sampling proportion	0.133 [-0.165, 0.464]	0.390	0.044 [-0.284, 0.386]	0.787
Trait phylogenetic signal	0.065 [-0.186, 0.321]	0.620	-0.001 [-0.270, 0.251]	0.987
Speciation rate variation	0.254 [-0.002, 0.511]	0.058	0.093 [-0.176, 0.349]	0.477
Body size rate variation	0.017 [-0.191, 0.249]	0.882	-0.041 [-0.285, 0.188]	0.733

Scenario	**Tree size (tips)**	***r* = ±1**	***r* = ±0.5**	***r* = 0**
Positive correlation	50	0.19 (0.12)	0.08 (0.10)	-
	150	0.24 (0.08)	0.11 (0.06)	-
	250	0.26 (0.08)	0.14 (0.06)	-
	500	0.35 (0.10)	0.16 (0.05)	-
Negative correlation	50	-0.18 (0.12)	-0.10 (0.10)	-
	150	-0.24 (0.08)	-0.12 (0.06)	-
	250	-0.26 (0.08)	-0.13 (0.06)	-
	500	-0.34 (0.10)	-0.16 (0.05)	-
No correlation (variable rates)	50	-	-	0.01 (0.10)
	150	-	-	0.00 (0.05)
	250	-	-	0.00 (0.04)
	500	-	-	0.00 (0.03)
No correlation (constant rates)	50	-	-	-0.01 (0.11)
	150	-	-	0.00 (0.06)
	250	-	-	0.00 (0.04)
	500	-	-	0.00 (0.03)