

INTEGRATING FOSSILS WITH MOLECULAR PHYLOGENIES IMPROVES INFERENCE OF TRAIT EVOLUTION

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Comparative biologists often attempt to draw inferences about tempo and mode in evolution by comparing the fit of evolutionary models to phylogenetic comparative data consisting of a molecular phylogeny with branch lengths and trait measurements from extant taxa. These kinds of approaches ignore historical evidence for evolutionary pattern and process contained in the fossil record. In this article, we show through simulation that incorporation of fossil information dramatically improves our ability to distinguish among models of quantitative trait evolution using comparative data. We further suggest a novel Bayesian approach that allows fossil information to be integrated even when explicit phylogenetic hypotheses are lacking for extinct representatives of extant clades. By applying this approach to a comparative dataset comprising body sizes for caniform carnivorans, we show that incorporation of fossil information not only improves ancestral state estimates relative to those derived from extant taxa alone, but also results in preference of a model of evolution with trend toward large body size over alternative models such as Brownian motion or Ornstein–Uhlenbeck processes. Our approach highlights the importance of considering fossil information when making macroevolutionary inference, and provides a way to integrate the kind of sparse fossil information that is available to most evolutionary biologists.

KEY WORDS: Ancestral states, Brownian motion, Caniformia, model selection, phylogenetic comparative methods.

“I am trying to pursue a science that is beginning to have a good many practitioners but that has no name: the science of four-dimensional biology or of time and life. Fossils are pertinent to this field when they are treated as historical records . . .” (Simpson 1953)

The last decade has witnessed a revolution in evolutionary biology. Fueled by the increased availability of time-calibrated molecular phylogenies (Drummond and Rambaut 2007) and new analytical tools for analyzing trait data, comparative biologists have increasingly switched their attention from describing evolutionary patterns and correlations to testing fundamental predic-

tions of macroevolutionary processes. The structure of phylogenies when combined with models of continuous trait evolution now allows biologists to address hypotheses about the manner in which standing phenotypic diversity was generated by testing for shifts in rates of trait evolution (O’Meara et al. 2006; Thomas et al. 2006; Eastman et al. 2011; Revell et al. 2012) or adaptive trait optima (Butler and King 2004; Beaulieu et al. 2012). Trait-dependent diversification models can also be used to determine the impact of those traits on lineage diversification (Maddison et al. 2007; FitzJohn et al. 2009; FitzJohn 2010). Tests for early bursts (EBs) of phenotypic and lineage diversification



consistent with classic adaptive radiation theory (Simpson 1944, 1953; Schluter 2000; Harmon et al. 2003; Gavrilets and Losos 2009) have been a particularly rich area of research (e.g., Pybus and Harvey 2000; Rabosky and Lovette 2008a, b; Harmon et al. 2010; Burbrink and Pyron 2010; Mahler et al. 2010; Slater et al. 2010).

As historical records of the evolutionary process, fossil taxa potentially provide a tremendous source of information regarding the tempo and mode of lineage diversification and trait evolution. However, the combining of paleontological and neontological (especially molecular) data into phylogenetic comparative methods has been slow and the full impact of fossil information on analyses of extant taxa remains relatively unexplored. A few studies have noted explicit conflict between inferences about lineage diversification rates derived from molecular phylogenies and those derived from the fossil record (Quental and Marshall 2009; Quental and Marshall 2010; Simpson et al. 2011; Rosenblum et al. 2012; see also Liow et al. 2010 for a simulation-based demonstration). Because paleobiologists and neontologists use different kinds of data to infer different aspects of net diversification rates (Foote 1996; Wagner 2000; Ricklefs 2007; Quental and Marshall 2010), this discordance is, perhaps, unsurprising and has primarily led to efforts to develop mathematical models that can better account for unobserved originations and extinctions in molecular phylogenies of extant taxa (e.g., Etienne and Apol 2009; Rabosky 2009; Morlon et al. 2011; Etienne et al. 2012).

For models of trait evolution, data integration is theoretically more straightforward. If fossil species with measured traits can be placed in a phylogeny, models of trait evolution can easily be fitted to data comprising fossil and extant taxa. It has long been recognized that incorporating information from fossil taxa in phylogenetic reconstruction based on morphological data (Felsenstein 1978; Donoghue et al. 1989; Gauthier et al. 1988; Huelsenbeck 1991) and in ancestral state reconstructions of quantitative traits (Oakley and Cunningham 2000; Finarelli and Flynn 2006; Alberts et al. 2009) can improve parameter estimates and overall method performance. The same should be true when comparing the fit of different models of quantitative trait evolution to comparative data, but this has not yet been thoroughly explored. Adapting current methods would require knowing both where the fossil connects to the tree and the branch length leading from the tree to the fossil. A significant barrier to incorporating fossil information in analyses of phenotypic evolution, however, is that we often only have very general ideas about their relationships to extant taxa. In these cases, integrating fossil information requires a different approach.

In this article, we explore, via simulation, the impact of fossil taxa on model selection when fitting models of quantitative trait evolution to comparative data. We then present a novel Bayesian approach that allows fossil data to be used to define informative

node priors when performing macroevolutionary analyses on extant taxa. We show that this approach performs well, even when prior distributions are not exactly centered on the true values, as might be the case when sampling from the incomplete fossil record. We finally apply this new approach to the case of body size evolution in caniform carnivores (Finarelli and Flynn 2006), and show using a modest number of informative node priors that incorporation of fossil information using our approach not only improves parameter estimates, but also results in the selection of a model with an evolutionary trend toward large body size that otherwise could not be detected with data derived from extant taxa.

Methods

MODELS OF TRAIT EVOLUTION

In this article, we consider four common models that have been applied to quantitative trait data. The first and most basic evolutionary model for continuous traits used by comparative biologists is Brownian motion (BM), which reasonably approximates evolution under drift or adaptive evolution tracking a randomly fluctuating optimum (Cavalli-Sforza and Edwards 1967; Felsenstein 1973, 1985; Hansen and Martins 1996). Under BM, the vector of trait values, \mathbf{X} , for a clade of n species follow a multivariate normal distribution,

$$\mathbf{X}_{(1,2,\dots,n)} \sim N(\mathbf{a}, \sigma^2 \mathbf{C}),$$

where \mathbf{a} is an $n \times 1$ vector in which each element is the expected value of the trait (which, under BM, is the root state a), σ^2 is the Brownian rate parameter and \mathbf{C} is an $n \times n$ covariance matrix, referred to as the phylogenetic variance–covariance matrix. The off-diagonal elements of \mathbf{C} , C_{ij} , represent the shared path length from the root of the phylogenetic tree to the most recent common ancestor of the i th and j th taxa, whereas diagonal elements C_{ii} represent the distance from the root node to the i th terminal taxon, which may be extant or extinct. Most alternative models of trait evolution, including the three that we consider in this article, are variants on this basic BM model that involve a transformation of \mathbf{a} , $\sigma^2 \mathbf{C}$ (also referred to as \mathbf{V}), or both. Under BM with a directional trend (Trend: Hunt 2006), variances and covariances remain the same but the expected value of the trait changes through time as function of a trend parameter, M , that can be positive or negative. Under a Brownian process with time-dependent rates, also referred to as AC/DC (Accelerating/Decelerating evolution: Blomberg et al. 2003), the rate of phenotypic evolution increases (AC) or decreases (DC) exponentially through time as a function of a parameter r that can vary between $-\infty$ and ∞ . The DC part of this model has also been called EB by Harmon et al. (2010). Finally, under an Ornstein–Uhlenbeck (OU) process, the

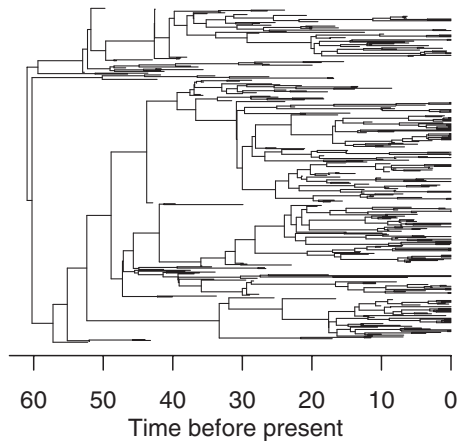


Figure 1. Phylogenetic tree used for simulations. The tree was generated under a birth–death process with birth rate = 0.1 and death rate = 0.09. There are 100 extant taxa and 277 fossil taxa.

elements of \mathbf{V} are transformed according to their distance from the basal split in the phylogeny and by a so-called “rubber-band” parameter, α (Hansen 1997; Butler and King 2004). Under OU, as a trait evolves away from its optimal value, it is pulled back toward the optimum with a strength corresponding to α . Although it is possible for the root state and trait optimum to differ, or for multiple trait optima (Butler and King 2004) or α values (Beaulieu et al. 2012) to exist, comparative methods often assume that the root state and optimum are the same, reducing OU to a single stationary peak (SSP) model (Harmon et al. 2010) that we will consider here. Useful summaries of these models and how they relate to BM can be found in Hunt (2006) and Harmon et al. (2010).

THE EFFECT OF FOSSIL TAXA ON MODEL SELECTION

We first assessed the impact of including fossil taxa with known phylogenetic placement and branch lengths on model selection performance. We generated a phylogenetic tree containing 100 extant taxa under a time-homogeneous, bifurcating birth–death process using the *geiger* package (Harmon et al. 2008) for R (R Development Core Team 2011). A tree of this size is large enough to potentially allow for differentiation of models of trait evolution (FitzJohn et al. 2009; FitzJohn 2010; Harmon et al. 2010; Boettiger et al. 2012) and is comparable to one that might be used in a typical empirical analysis of extant taxa. To generate a tree with a large number of extinct tips, we simulated under a birth–death process with high relative extinction rate ($\lambda = 0.1$, $\mu = 0.09$). The resulting tree had a total of 377 taxa, with a root age of 60.95 time units (Fig. 1). To avoid confounding variation due to fossil inclusion with variation associated with phylogenetic tree shape, we focus here on analyses from a single simulated tree. Results from fitting models to alternative phylogenetic trees were always qualitatively consistent, although we note that overall,

Table 1. Parameter values and sampled ranges used for simulation tests. Under Trend, the parameter is μ , the trend parameter. Under SSP, the parameter is α , the strength of selection. Under AC/DC, the parameter is r , the exponential change parameter.

Model	A	σ^2	non-BM parameter
BM	0	$U[0, 0.5]$	–
Trend	0	0.1	$U[0, 0.2]$
SSP	0	0.1	$U[0.01, 10]$
AC	0	0.0013	$U[0, 0.1]$
DC	0	0.13	$U[-0.1, 0]$

fossils improve model selection more when extinction rates are higher (see Appendix S1 for full details). We next simulated trait evolution on the complete 377-taxon tree under the four models of trait evolution: BM, Trend, AC/DC, and SSP. To explore the effects of varying model parameters on model selection with or without fossil information, we simulated 500 datasets under each model, with model parameters drawn at random from uniform ranges (Table 1). The root state was fixed at $a = 0$ for simulations under all models. For BM, we varied the rate parameter σ^2 . For all other models, we fixed σ^2 and varied the model-specific parameter as specified in Table 1. To fully explore model-fitting performance, we treated AC/DC as two separate models (AC and DC) for simulation purposes.

For each set of simulations, we initially fit the four models to datasets comprising extant taxa only using maximum likelihood (ML). We then repeated this procedure five times, each time randomly adding 5%, 10%, 25%, 50%, and 100% of the total number of fossil taxa to the dataset. Model fitting was done using the *fitContinuous* function in *geiger* (Harmon et al. 2008). For each level of fossil sampling, we compared support for the four models using small-sample corrected Akaike weights (AIC_c ; Burnham and Anderson 2002), where the sample size equals the number of sampled terminals in the phylogeny, including fossils when applicable. If fossils have a positive effect on model selection, then Akaike weights for the true model should increase as more fossil taxa are added.

The addition of fossil taxa to a dataset comprising extant taxa, as described above, increases the total number of taxa. Thus, any improvement in model-fitting performance could be attributable to a larger net sample size, rather than just the inclusion of fossil taxa. We therefore also investigated whether, given a fixed sample size of taxa, we should prefer to sample fossils or extant taxa. We repeated the model-fitting procedure described above but randomly substituted proportions of extant taxa for fossil taxa, rather than adding them, thus maintaining a total of 100 taxa. We repeated this procedure for proportions of 5%, 10%, 25%, 50%, and 95% of the total number of extant species, using 95% rather than 100% in the final step so that the resulting tree maintained

the same root-tip distance without rescaling of branch lengths. Model support was again assessed using AIC_c weights.

USING FOSSILS AS NODE PRIORS

For most comparative biologists, phylogenetic information is typically lacking for fossil members of their study clade. In these cases, integrating available fossil information requires a different approach to ML. Under the multivariate normal distribution, the log-likelihood for a set of observed trait values \mathbf{X} is computed as

$$\ln(L) = \ln \left(\frac{\exp \left\{ \frac{1}{2} [\mathbf{X} - \mathbf{E}(\mathbf{X})]' (\mathbf{V})^{-1} [\mathbf{X} - \mathbf{E}(\mathbf{X})] \right\}}{\sqrt{(2\pi)^n \cdot \det(\mathbf{V})}} \right),$$

where $\mathbf{E}(\mathbf{X})$ is a $n \times 1$ vector of expected trait values, prime specifies that the transpose is taken, and \mathbf{V} is the model-specific variance-covariance matrix (O'Meara et al. 2006; Harmon et al. 2010). Normally, only trait values for the terminal taxa are represented in this expression; likelihood approaches to fitting models of trait evolution avoid explicit reconstruction of trait values at nodes other than the root by integrating parameter estimates over all possible ancestral states (Pagel 1994, 1997; Schluter et al. 1997). In a Bayesian framework, this is equivalent to assuming a uniform prior density on each ancestral state, with the result that their posterior densities are directly proportional to the likelihood surface (Maddison 1991; Schluter et al. 1997). However, if we lack precise phylogenetic information regarding the placement fossil taxa but they can be associated with particular nodes in a molecular phylogeny, then their traits could be used to inform prior distributions placed on those nodes when fitting models to datasets comprising extant taxa.

We implemented a Markov chain Monte Carlo (MCMC) algorithm to sample trait evolutionary model parameters and node values from their posterior distributions while allowing informative prior distributions to be placed on nodes with associated fossil taxa. At each step in our MCMC sampler, we propose model parameters and ancestral states, and assess the posterior probability of the model as the product of the likelihood and prior probabilities of proposed parameters and ancestral states. The decision to accept or reject proposed parameters are made using the standard Metropolis-Hastings algorithm (Metropolis et al. 1953; Hastings 1970). R code to perform these analyses is contained in the function `fitContinuousMCMC()`, which will be available via CRAN in a forthcoming release of the `geiger` library, and is available in the short term as a package download from LJH's software page (<http://www.webpages.uidaho.edu/~lukeh/software/index.html>).

To test this approach, we performed five MCMC runs with each set of simulations (see above) under each of the four models of evolution. In the first set of runs, the four models were fitted to the simulated data with uninformative priors on all node states.

We subsequently performed runs where informative normal prior distributions were applied to random samples of 5%, 10%, 25%, and 50% of nodes in the tree, excluding the root node. For each node, the mean of the prior was set to the true node value taken from the simulated data, and the standard deviation (SD) was set at an arbitrarily small value of 0.01. In Appendix S1, we present results from an additional test of our approach using node priors sampled from a simulated fossil. In these tests, informative node priors were defined based on fossil taxa that (1) were descendants of the immediate parent node to the node of interest and (2) went extinct within a 10 million year window centered on that node. As a result of this sampling scheme, not all nodes possessed informative priors, and those that did had priors that were not necessarily centered exactly on their true values. Furthermore, some priors were defined based on only a few fossils with distant phylogenetic relationships to the focal node (see Appendix S1 for more details). For both sets of analyses, nodes were sampled at random among simulations and sampling schemes. We set uninformative priors of $U[-\infty, \infty]$ on α , $\ln(\sigma^2)$ and the remaining nodes for each model, and on M for the Trend model. For SSP, we used a uniform prior on α of $[10^{-5}, \infty]$. For AC/DC, we applied a uniform prior $U[-0.5, 0.5]$ to the exponential change parameter, r . Each analysis was run for 200,000 generations, sampling from the chain every 100 steps, with the first 25% of samples discarded as burn-in. For each fossil sampling regime, the three non-Brownian models were compared to BM using Bayes factors computed from harmonic means of the sampled likelihoods (Newton and Raftery 1994; Kass and Raftery 1995). To assess false-positive rates, that is, cases in which we select an incorrect model with strong support, we assumed that a value for $2^* \ln(\text{Bayes factor})$ of 2 or greater indicated positive support for that model over the null, BM model (Kass and Raftery 1995; Raftery 1996).

Results

THE EFFECT OF FOSSIL TAXA ON MODEL SELECTION

Adding fossil taxa with known phylogenetic placement and branch lengths had a great impact on model selection performance, but only when the true model deviated from pure BM. When BM was the true model, we found low power to favor it over other candidate models based on extant taxa only. Adding fossils had no effect on model selection for any value of σ^2 (Figs. 2A, S6A; Table S3). For the other models, adding fossil taxa increased both the overall power to detect the true model and the power to do so at small parameter values (i.e., those resulting in a model most similar to BM) compared to fits using extant taxa only. A particularly striking result was recovered when the true model was accelerating evolution. Here, AC was never favored over other models using extant taxa only (Figs. 2D, S6M;

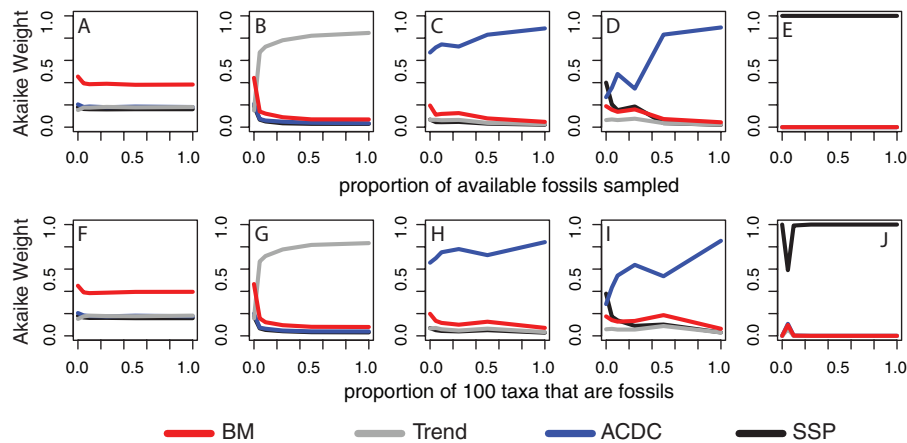


Figure 2. Median Akaike weights for the four evolutionary models fitted by maximum likelihood to 500 datasets. Datasets were simulated under BM (A, F), Trend (B, G), DC (C, H), AC (D, I) and SSP (E, J). In the top row (A–E), increasing proportions of the 277 available fossils were randomly added to the 100-tip ultrametric tree. In the bottom row (F–J), proportions of extant taxa were replaced with fossils.

Table S3). Instead, BM was favored at low increases in rate and SSP at higher increases (Fig. S6M). The addition of fossils dramatically increased support for the correct model of AC/DC while simultaneously reducing support for SSP and BM (Figs. 2D, S6N–P).

We found that swapping extant taxa for fossils while maintaining a constant total number of taxa also resulted in improved model selection performance, relative to analyses based on extant taxa only. This result suggests that on a per-taxon basis, fossils contain more information regarding the mode of trait evolution than do extant taxa. When BM was the true model, Akaike weights for BM remained slightly higher than those for the alternative models, but still ambiguous under all levels of fossil swapping (Figs. 2F, S7A–D; Table S4). For all other models, swapping fossils for extant taxa both increased support for the true model relative to other models and the power to discern them at low parameter values (Figs. 2H–J, S7E–T; Table S4). One notable exception was found when the true model was SSP. In this case, weights for SSP decreased from a median weight of 1 when no fossils were sampled to a median weight of 0.59 with 5% replacement of extant taxa by fossils (Fig. 2J; Table S4). This result may reflect the observations that: (1) SSP and AC are difficult to distinguish without fossil information, and/or (2) without fossils, SSP tends to be favored over AC, regardless of which is the true model. Reducing the number of extant taxa and adding a few fossils seems to have the effect of accentuating this uncertainty. However, increasing the proportion of fossils swapped to 10% increased median weights for SSP to 0.99, suggesting that high levels of fossil sampling are not necessary to increase confident identification of the true model.

USING FOSSILS AS NODE PRIORS

When BM was the true model, there was very little power to distinguish it from the three alternative models using Bayes factor comparison with uninformative priors on all node states. As with ML estimates, BM could not be rejected however (Fig. 3A). There was still power to distinguish the three other models from BM using uninformative node priors, particularly when parameter values were large (Fig. 3G, J, M). When SSP was the true model, it could be readily distinguished from BM at all values of α , although AC also received positive, albeit lower support over BM. When AC was the true model, we found it to be indistinguishable from SSP, even at large values of r , although both received positive support relative to BM.

Addition of informative priors on node values improved model selection performance in all cases except where BM was the true model (Fig. 3B, C). BM remained indistinguishable from the alternative models at all values of node sampling, and false-positive rates did not decrease appreciably, except for comparisons of SSP to BM (Table 2). For the other models, addition of priors on node values increased power to identify the true model, with increasing numbers of priors markedly increasing power at low parameter values (Fig. 3). The most notable result was recovered when the true model was AC. Although AC and SSP were equally favored over BM based on extant taxa alone, addition of fossil information in the form of node priors resulted in increased support for the true model (AC), while support for SSP decreased. Similarly, increasing the number of nodes with informative priors increased support for SSP while decreasing support for AC when SSP was the true model. In Appendix S1, we show that our approach also performs well using informative priors derived from

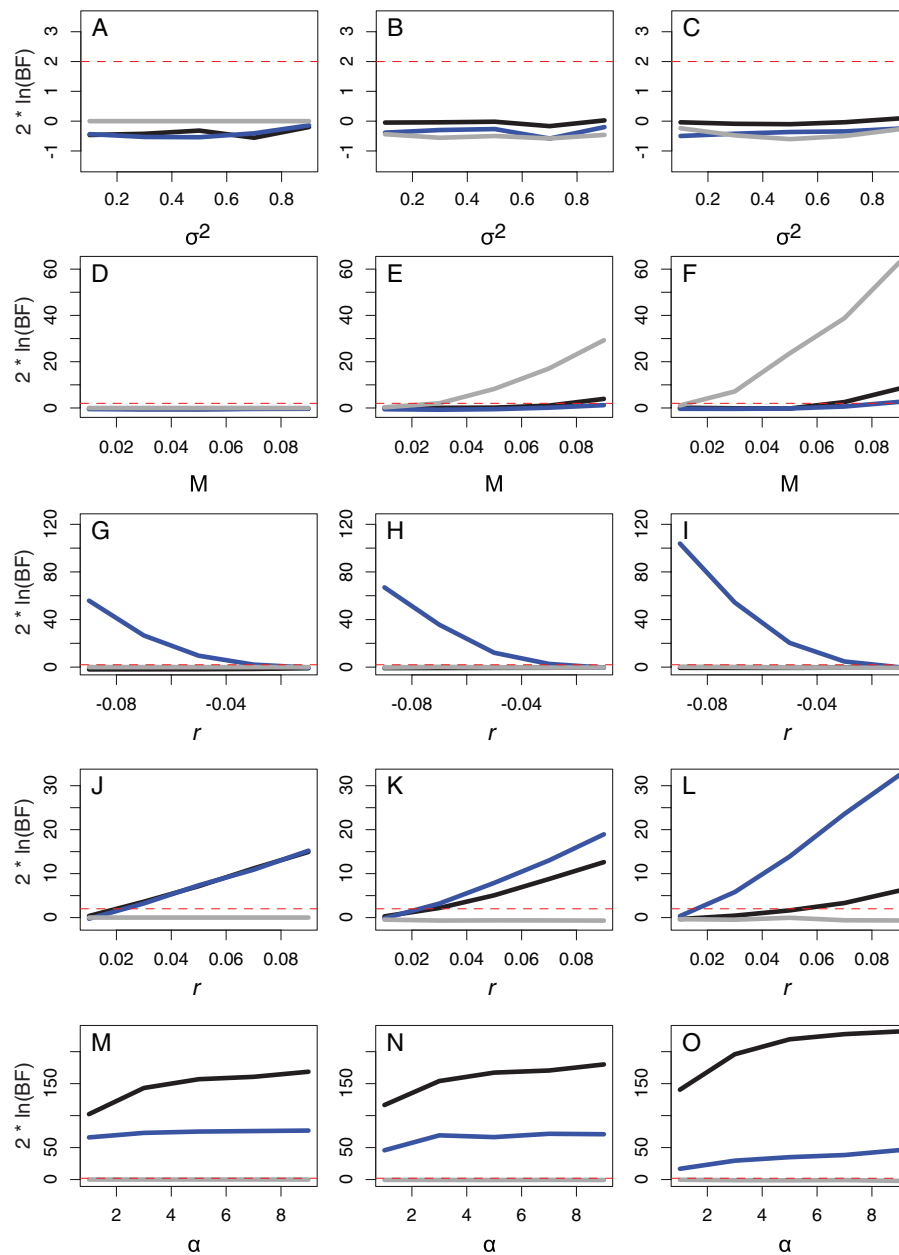


Figure 3. Median Bayes factors for candidate models fitted to 500 simulated datasets with informative node value priors on 0, 10, and 50% of total nodes in the tree. In each case, candidate models are compared to a null model of Brownian motion. Rows represent simulations under BM (A–C), Trend (D–F), DC (G–I), AC (J–L), and SSP (M–O). In each panel, the x-axis represents the range of model parameter values simulated under, whereas plotted lines represented the medians of binned Bayes factors. Line colors are Trend (gray), AC/DC (blue), and SSP (black), all compared to BM. The dashed red line indicates the Bayes Factor required to achieve positive evidence in favor of a given candidate model.

a simulated fossil record, despite the fact that priors were derived from a small number of fossils that were often younger than the node of interest.

BODY SIZE EVOLUTION IN CANIFORM CARNIVORANS

To illustrate the application of our Bayesian approach to an empirical dataset, we revisited the case of body size evolution in can-

iform carnivores (Finarelli and Flynn 2006). Morphological and ecological diversity within the Caniformia is particularly striking; caniforms range from exclusive herbivores to specialist carnivores (Figueirido et al. 2010) and span the entire range of body sizes encompassed by extant Carnivora (over four orders of magnitude). Finarelli and Flynn (2006) demonstrated that unreasonably large estimates (~ 25 kg) for the ancestral body size of caniforms were obtained when only extant taxa are considered. However, when

Table 2. False-positive rates for Bayesian model selection using node value priors centered on the true node value. False positives under three Bayes factor cut-offs are given.

Prop. nodes	$2 \times \ln BF = 2$			$2 \times \ln BF = 6$			$2 \times \ln BF = 10$		
	Trend	AC/DC	SSP	Trend	AC/DC	SSP	Trend	AC/DC	SSP
0	0.00	0.11	0.11	0.01	0.01	0.01	0	0	0
0.05	0.09	0.11	0.07	0.01	0.01	0.01	0	0	0
0.1	0.09	0.12	0.07	0.01	0.01	0.01	0	0	0
0.25	0.09	0.11	0.07	0.01	0.01	0.01	0	0	0
0.5	0.10	0.12	0.07	0.01	0.01	0.01	0	0	0

fossil taxa were included in their phylogeny, more reasonable ancestral size estimates of ~ 5 kg were obtained. Finarelli and Flynn (2006) suggested that this might be the result of an evolutionary trend toward large body size (Cope's rule, e.g., Alroy 1998; Purvis and Orme 2005) in some extant families. We therefore asked whether the incorporation of fossil information into a comparative dataset derived from extant caniform carnivorans could provide support for this model over other candidate models of body size evolution.

CANIFORM METHODS

Body mass data for extant caniform species were obtained from the panTHERIA database (Jones et al. 2009), with missing species added from the literature where possible. We initially attempted to use the carnivoran portion of the mammalian supertree (Bininda-Emonds et al. 2007). However, attempts to identify fossil taxa that could be phylogenetically and temporally associated with nodes in that tree revealed some significant discrepancies in topology and divergence times compared with current understanding of carnivoran phylogeny (Bardeleben et al. 2005; Flynn et al. 2005; Koepfli et al. 2007; Koepfli et al. 2008; Krause et al. 2008; Eizirik et al. 2010; Fulton and Strobeck 2010a, b; Meredith et al. 2011). We therefore constructed a new time-calibrated phylogeny for caniforms by grafting published and new time-calibrated phylogenies for caniform clades onto a family-level backbone tree (Eizirik et al. 2010). Full details of phylogeny reconstruction are provided in Appendix S2 and .xml files have been deposited on Dryad. After removing nonoverlapping species from the tree and body size data, we retained a final sample of 135 taxa, approximately 82% of extant caniform diversity (Fig. 4). We subsequently surveyed the literature for fossil taxa that could be associated with nodes in the caniform phylogeny, where possible giving preference to fossils that had been subject to phylogenetic analyses. We used published estimates of body mass when available, but otherwise estimated body masses for fossil taxa from lower first molar lengths, using regression equations provided in Van Valkenburgh (1990). Informative node value priors were derived from means and SDs computed from natural log-transformed fossil masses.

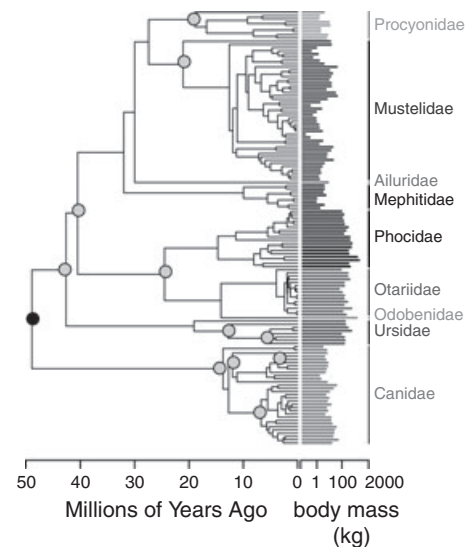


Figure 4. Time-calibrated phylogeny of 135 species of extant caniforms and associated body masses (note that bar lengths are represented on a log scale). Colors indicate caniform families. Gray circles at nodes indicate locations of fossil priors used for fitting models of body size evolution. The black node label indicates the root prior.

The final set of priors spanned 11 internal nodes, plus the root node (Fig. 4; Table 3). Body masses for individual fossil taxa used to define informative node priors are provided in Table S7.

We first compared the fit of three models of trait evolution (BM, AC/DC, SSP) with uninformative priors placed on all node values. Two chains were run for 500,000 generations each, sampling from the chain every 100 steps, and the first 10% of samples from each run as burn-in based on inspection of likelihood trace plots. Marginal likelihoods and parameter values were computed from the retained sample. We then re-ran analyses using the same MCMC procedures but with informative normal prior distributions placed on the 11 internal nodes with associated fossil information. For these analyses, the Trend model was added to the suite of models fitted. Because fossil information was available for the root node of caniform phylogeny, we performed a third

Table 3. Priors used for fitting models of trait evolution to the caniform dataset. Means and standard deviations are in units of natural log (Ln) kilogram.

Node	Mean	SD
Root node	0.749	0.485
MRCA Caninae	1.451	0.487
MRCA Vulpini	1.974	0.29
MRCA Vulpes	1.831	0.211
MRCA Canini	2.225	0.184
MRCA Arctoidea	0.615	0.336
MRCA Ursinae/Tremarctinae	4.293	0.129
MRCA Ursinae	4.406	0.028
MRCA crown Mustelidae	1.296	0.4645
MRCA crown Procyonidae	0.417	0.172
MRCA Pinnipedimorpha+Musteloidea	1.14	0.33
MRCA crown Pinnipedia	4.111	0.957

set of analyses with priors on the 11 internal nodes plus the root node.

CANIFORM RESULTS

Fossils had a significant impact on root state estimation (Fig. 5). With uninformative priors on all internal nodes, we estimated a large body mass (~18.5 kg) for the ancestral caniform under all models, albeit with wide 95% highest posterior density intervals (HPD: 1.85–171 kg; Fig. 5). Fitting the same models with informative prior distributions on 11 internal nodes resulted in substantially smaller modal estimates (~2.5 kg) and narrower 95% HPD intervals for the root state (0.34–10 kg; Fig. 5). Addition of a root node prior unsurprisingly resulted in narrower still 95% HPD intervals (0.89–4.5 kg), although the mode did not shift. Overall, these results are consistent with those of Finarelli and Flynn (2006) and appear to suggest a non-Brownian model of body size evolution in caniform carnivorans.

Fossils also had an impact on model selection for the caniform body size dataset. With uninformative priors on all nodes, BM, AC/DC, and SSP were broadly indistinguishable (Table 4). The addition of fossil-derived priors on 11 internal nodes had little effect on comparisons between these three models, but did lead to positive ($2 \times \ln BF > 2$) support for Trend over BM. Addition of a prior on the root state had little impact on model selection compared with results obtained using internal node priors only (Table 4).

Although we find positive evidence for a trend toward increasing body size in caniform evolution, support for this model over BM is relatively low. One possible reason for this is the interacting effect of the strength of the trend and the proportion of nodes for which we had available prior information. Our estimates for the Trend parameter were low ($M = 0.0296$, 95%

HPD: -0.002 – 0.063), which is approximately equivalent to a net expected increase in size of ~7 kg over the 50 million year history of extant caniforms. Based on simulations, a trend of this magnitude is difficult to favor with positive evidence or greater with informative priors on only 10% of nodes (Fig. 3E; Appendix S1). The fact that we find positive evidence in favor of Trend with only 8% of available nodes sampled is therefore encouraging. It is also worth noting that the Trend model used here assumes a homogenous directional trend across all lineages through time (Hunt 2006). This might be expected under a phenomenon such as Cope's rule where an active trend drives all clade members toward larger size (Alroy 1998; Van Valkenburgh et al. 2004; Purvis and Orme 2005). However, it is possible that the evolution of caniform body sizes is better explained by a passive trend, such as diffusion away from a reflective or absorbing lower bound (Stanley 1973; Gould 1988; Alroy 2000). Although such an argument makes sense on physiological grounds (Tracy 1977; West et al. 2002), it cannot currently be tested using phylogenetic comparative models.

Discussion

Fitting models of quantitative trait evolution to phylogenetic comparative data provide a powerful way of testing fundamental hypotheses about macroevolutionary pattern and process (Hansen 1997; Blomberg et al. 2003; Butler and King 2004; O'Meara et al. 2006; Thomas et al. 2006; Thomas et al. 2009; FitzJohn 2010; Harmon et al. 2010; Eastman et al. 2011; Revell et al. 2012; Slater et al. 2012). All too frequently however, analyses are limited to extant taxa, neglecting the historical information that fossil data can provide (Simpson 1944, 1953; Losos 2011). The results presented in this study suggest that inclusion of just a few fossil taxa not only increases the statistical power of these approaches, but can also lead to differentiation of models that simply cannot be distinguished based on extant taxa data alone. Furthermore, although many clades lack a well-sampled fossil record (a point we will return to at the end of this article), we have shown how sparse fossil information without phylogenetic resolution can be integrated into macroevolutionary analysis in a way that can still improve model selection over estimates based on extant taxa only.

DO FOSSILS IMPROVE ESTIMATES OF TRAIT EVOLUTION?

We found that fossils had little effect on model selection when BM was the generating model of evolution. Instead, the greatest impact of fossils is realized when the generating model is a time-heterogeneous processes. One possible explanation for this result is that our model comparison metric, Bayes factors derived from the harmonic mean estimator (HME) of the marginal likelihood, is a poor model selection tool. Recent work in demographic

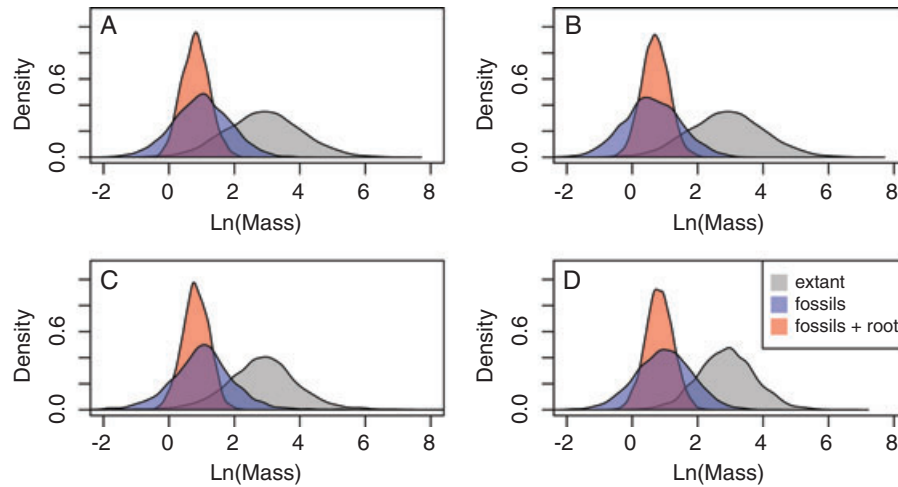


Figure 5. Posterior distributions for the root node state in the caniform example estimated under BM (A), Trend (B), AC/DC (C), and SSP (D). Colors represent MCMC analyses with and without fossil information incorporated as informative node priors.

Table 4. Results of model fitting for the caniform dataset with no priors, with node priors, and with node and root priors. Marginal likelihoods are given for all models except Trend with no priors, which cannot be distinguished from BM. Bayes factors are computed for models relative to BM. Asterisk indicates positive evidence in favor of the candidate model over BM.

	No priors		Node priors, no root prior		Node priors, root prior	
	Marginal Lk	$2 \times \text{LnBF}$	Marginal Lk	$2 \times \text{LnBF}$	Marginal Lk	$2 \times \text{LnBF}$
BM	-169.61	–	-178.72	–	-178.36	–
Trend	–	–	-177.33	2.77*	-177.02	2.69*
SSP	-169.54	0.13	-178.74	-0.05	-178.64	-0.55
ACDC	-169.83	-0.44	-179.17	-0.90	-178.73	-0.74

and phylogenetic model selection has demonstrated that this can sometimes be the case (Xie et al. 2011; Baele et al. in press). Alternative metrics, such as AICM (Raftery et al. 2007), and path sampling (thermodynamic integration: Lartillot and Philippe 2006) and stepping-stone (Xie et al. 2011) algorithms can outperform HME estimators in many cases (Baele et al. in press). The integration of Bayesian approaches into phylogenetic comparative methods is still in its infancy, but further work on model selection procedures has the potential to greatly increase power to discern among models of quantitative trait evolution (see also Boettiger et al. 2012).

The most obvious impact of adding fossil data was for the case of the Trend model, where the expected value of a trait increases or decreases as a function of time. Identification of a trend is therefore explicitly dependent on knowledge of both the starting and end states. If a directional trend exists in comparative data, our ability to accurately infer the ancestral state for the trait from data derived from extant taxa only is lost as the trait evolves away from its initial state (e.g., Oakley and Cunningham 2000; Finarelli and Flynn, 2006; Albert et al. 2009). As a result, we completely lack the ability to fit the Trend model without some

fossil information (it should be noted however that a strong prior on the root state would be sufficient to allow this model to be fitted; Oakley and Cunningham 2000; see also Felsenstein 1988). The improved power for the other models fitted here is similarly a function of their time dependency. It would be interesting to further investigate the impact of fossils when fitting models allowing for components of punctuated (i.e., speciation) and gradual (i.e., Brownian) evolution (Hunt 2007b, 2008; Bokma 2008).

We found that without fossils, the power to discern decelerating evolution was greater than that for accelerating evolution. This makes sense given the differing expectations of these opposing processes. Decelerating evolution results in phenotypic disparity being partitioned among rather than within clades, a pattern that can be readily identified from extant taxa data when the difference between initial and end rates is large enough (Harmon et al. 2003). Adding fossils provides additional information about the tempo at which disparity evolves and thus further allows for differentiation of slow deceleration from a constant rates process (Figs. 2, 3, S3, S6, S7). Under accelerating evolution, in contrast, faster evolution toward the tips result in increased within-clade disparity relative to among clade disparity—a pattern also seen under

the SSP model. Our results suggest that accelerating evolution is difficult to distinguish from BM with a fast rate based on extant taxa alone unless the magnitude of acceleration is relatively large. In such cases, however, accelerating evolution becomes difficult to distinguish from SSP.

Fossil information dramatically improved our ability to distinguish SSP and AC. Accelerating evolution results in rapid evolutionary change along branches closer to the tips of a phylogeny, with the net result that recent species possess markedly different trait values than their sister species. Looking at extant taxa only, the outcome of this process is very similar to an OU process, as both tend to erase phylogenetic signal (Revell et al. 2008). The incorporation of data from fossil taxa provides a source of historical information regarding character change toward the root the tree and thus enables these two models to be distinguished. This result is particularly interesting given that Harmon et al. (2010) found a prevalence of signal for SSP over BM and DC (or “EB”) in a large number of comparative datasets. Those authors suggested that the EB pattern expected under adaptive radiation hypotheses (Simpson 1944, 1953) might be rare in comparative data and that stabilizing selection might be a more pervasive pattern. Adding fossil information is unlikely to swing a preferred SSP model to DC; however, we are unable to rule out that a pervasive pattern of accelerating evolution is obscured in these datasets. Accelerating evolution might occur in adaptively radiating clades that have yet to saturate ecomorphospace, for example, as a young clade radiates to replace a waning, ecologically equivalent clade (e.g., Van Valkenburgh 1999). If diversifying clades are characterized by these kinds of patterns, then fossil information is of an even greater significance in providing insight into the dynamics of adaptive radiation.

USING FOSSILS AS NODE PRIORS

We also showed that trait data from fossil taxa can be meaningfully incorporated into comparative analyses as informative prior distributions on node values. This is particularly appealing as fossil representatives of extant clades are infrequently placed in an explicit phylogenetic context. Moreover, even when fossils can be placed in a phylogeny, branch lengths are typically not available (but see Pyron 2011), rendering fitting of time-dependent processes difficult. Felsenstein (2002) suggested an approach by which fossil taxa could be placed in a molecular phylogeny and their branch lengths inferred using their continuous trait values. In this scheme, fossils would be placed by maximizing the likelihood of the BM process given knowledge of the phylogeny of extant taxa, as might be inferred from molecular data. Although Felsenstein described this algorithm with a view toward phylogenetic inference rather than model fitting (a form of “Total Evidence”: Felsenstein 2002, p. 32), it could potentially be applied to the problem that we have attempted to solve. The approach we have

used here, in contrast, makes explicit use of synapomorphy-based assessment of fossil placement that is more familiar to evolutionary biologists from divergence time estimation (Drummond and Rambaut 2007), and has more in common with approaches, such as ancestor-descendent comparison, that have been traditionally been used in paleobiological inference (Gingerich 1987; Hulbert 1993; Wagner 1996; Alroy 1998; Van Valkenburgh et al. 2004; Hone et al. 2005). Our results show that most power is obtained when fossils are placed in as precise a phylogenetic context as possible. If this is not possible, then using fossils as priors on node states is still preferable over approaches that ignore fossil information entirely.

A pervasive concern in the use of Bayesian approaches is that inappropriate or incorrect priors can dominate the analysis, leading to misleading signal. Careful selection of fossils temporally spanning either side of a node of interest should ameliorate any tendency toward biased or incorrect priors (see Supporting Information). It should also be noted that our approach allows for the same fossil to be used in defining more than one prior. For example, a fossil might be the oldest member of a crown group while also being a stem representative of a more inclusive clade. In this case, the same fossil could be used when defining the distributions placed on both nodes. A logical extension of our method would be to use the temporal proximity of a fossil or set of fossils to determine the strength of the prior placed on a node. Using information in this way should lead to more appropriate priors and makes more complete use of potentially sparse available data.

One limitation of our approach is that fossil diversity from radiations along stem lineages will be mostly unusable if the entire stem group has gone extinct. For example, although we were able to associate fossil taxa with 12 nodes in the phylogeny of extant caniforms, we were unable to include information from the extinct canid subfamilies Hesperocyoninae and Borophaginae, the entire family Amphicyonidae, and the majority of fossil members of the extant, monotypic families Odobenidae (walrus) and Ailuridae (red panda), despite the fact that all possess good-to-excellent fossil records (Deméré 1994; Wang 1994; Hunt 1998; Wang et al. 1999; Morlo and Peigné 2010). Given that biologically reasonable values for most evolutionary model parameters are likely to be at the lower end of their respective scales, we potentially surrender tremendous statistical power by not including this available information. Reassuringly, both our simulations and our empirical example demonstrate that if a trend in trait values or time-dependency of rates actually exists, we retain substantial power to detect this with a sample of extant taxa and a set of informative node priors derived from suitable fossil data. For more complex models of trait diversification however, explicit phylogenetic hypotheses or alternative approaches for integrating phylogenetically uncertain fossil radiations are likely to be necessary.

BROADER IMPLICATIONS—FOSSILS, PHYLOGENIES, AND COMPARATIVE METHODS

Although the main message of this article is a statistical one—that incorporation of fossil information can improve model selection—our results raise a broader conceptual point regarding the utility of phylogenetic comparative methods. While discussing some limitations of phylogenetic methods, Losos (2011) argued that their use might introduce errors of unknown effect or magnitude because many traits do not exhibit phylogenetic signal. Although this observation may well be true, even where a trait appears to lack phylogenetic signal its evolution was still framed by the phylogenetic covariation among lineages in the clade of interest (Revell et al. 2008). Our simulation results suggest that incorporation of fossil data into comparative analysis where there is seemingly no phylogenetic signal can uncover phylogeny-wide trends in the tempo of trait evolution. For example, our approach can differentiate SSP from AC, two models which both produce relatively low levels of “phylogenetic signal” among extant taxa.

What do our results mean for future macroevolutionary studies when the fossil records of the most striking examples of adaptive radiation, such as East African rift lake cichlids, Caribbean anoles, Galapagos finches, and Hawaiian silverswords (Schluter 2000), are at best limited and at worst completely lacking (Harmon et al. 2010)? The answer to this question is complex and context dependent, but we suggest two generalizations can be made. First, in many respects, our results do not limit the significance of these systems. The fundamental prediction of adaptive radiation theory, at least in its classical context (Simpson 1944, 1953), is that clades should exhibit EBs of lineage and trait diversification as they rapidly radiate to fill new adaptive zones (Harmon et al. 2003). Although it is becoming clear that our ability to detect diversity-dependent lineage diversification from molecular phylogenies of extant taxa alone is limited over large temporal scales (Liow et al. 2010; Quental and Marshall 2010; Morlon et al. 2011; Etienne et al. 2012), the same does not appear to hold true for EBs of trait evolution, making this a promising avenue for future work on rapid radiations (Mahler et al. 2010; Slater et al. 2010; Dornburg et al. 2011). Because many of these flagship clades were recognized as putative adaptive radiations due to their exceptional phenotypic diversity and patterns of convergence, their lack of fossil records might not be a great impediment to continued study of their adaptive diversification. With this said, our results also suggest that the most comprehensive picture of tempo and mode in macroevolution will be painted using clades that possess relatively complete molecular phylogenies and well-sampled fossil records. These kinds of datasets are likely to be limited to taxa that possess robust fossilizable elements, such as mammals, or small marine taxa that are abundant in highly fossiliferous deposits (e.g., Webster et al. 2004; Hunt 2007a; Aze et al.

2011; Ezard et al. 2011). Although these taxa were instrumental in the development of macroevolutionary theory in the first half of the 20th century (Simpson 1944, 1953), they have been largely neglected in recent years. A return to these model systems therefore seems well overdue.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Histogram showing the sum distance of fossil taxa from their associated nodes under the simulated sampling scheme.

Figure S2. Akaike weights relative to extinction rate for each of the four models fitted to datasets simulated under BM, Trend, DC, AC, and SSP (columns).

Figure S3. Bayes factors with informative node priors derived from simulated fossil records.

Figure S4. Histogram of fossil taxa numbers used to define node priors based on the simulated fossil record.

Figure S5. Plot of the gamma statistic against extinction rate for a sample of simulated trees.

Figure S6. Median Akaike weights for each of four candidate models fitted to 500 datasets (see main text) simulated under BM (A–D), Trend (E–H), DC (I–L), AC (M–P), and SSP (Q–T).

Figure S7. Median Akaike weights for each of four candidate models fitted to 500 simulated datasets (see main text).

Figure S8. Time-calibrated phylogeny of the Canidae reconstructed and used for this analysis.

Figure S9. Time-calibrated phylogeny of the Otariidae reconstructed and used for this analysis.

Figure S10. Majority rule consensus trees from Bayesian analyses of molecular and morphological data for living and fossil Mephitids with (A) Mk+G and (B) Mk + unequal state frequencies for the morphological partition.

Figure S11. Time-calibrated phylogeny of Mephitidae reconstructed and used in this analysis.

Figure S12. Majority rule consensus trees from Bayesian analyses of molecular and morphological data for living and fossil Procyonids with (A) Mk+G and (B) Mk + unequal state frequencies for the morphological partition.

Figure S13. Time-calibrated phylogeny of Procyonidae reconstructed and used in this analysis.

Table S1. Correlation coefficients between Akaike weights for the true model of trait evolution and extinction rates of the phylogenies on which traits were simulated.

Table S2. False-positive rates for Bayesian model selection using node value priors derived from a simulated fossil record.

Table S3. Median Akaike weights over all parameter values under each fossil sampling level for the five sets of simulations.

Table S5. Sampled loci and Genbank accession numbers for the otariid analysis

Table S6. Sampled loci and Genbank accession numbers for the Mephitid analysis

Table S7. Fossil taxa used to define informative priors on node states when fitting models of quantitative trait evolution to the caniform dataset.

Supporting Information may be found in the online version of this article.

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