

Diversification Declines in Major Dinosaurian Clades are not Because of Edge Effects or Incomplete Fossil Sampling

Manabu Sakamoto

University of Lincoln <https://orcid.org/0000-0001-6447-406X>

Michael Benton (✉ Mike.Benton@bristol.ac.uk)

University of Bristol <https://orcid.org/0000-0002-4323-1824>

Chris Venditti

University of Reading <https://orcid.org/0000-0002-6776-2355>

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Abstract

Signatures of catastrophic mass extinctions have long been reported to be obscured by the edge effect where taxonomic diversity appears to decline gradually. Similarly, models of diversification based on splitting of branches on a phylogenetic tree might also be affected by undersampling of divergences towards the edge. The implication is that long-term declines in diversification recovered from such models – e.g., in dinosaurs – may be artefacts of unsampled divergences. However, this effect has never been explicitly tested in a phylogenetic model framework – i.e., whether phylogenetic nodes (speciation events) close to the edge are under-sampled and if diversification declines are artefacts of such under-sampling. Here, we test whether dinosaur species in temporal proximity to the Cretaceous-Paleogene mass extinction event are associated with fewer nodes than expected, and whether this under-sampling can account for the diversification decline. We find on the contrary that edge taxa have higher numbers of nodes than expected and that accounting for this offset does not affect the diversification decline. We demonstrate that the observed diversification declines in the three major dinosaurian clades in the Late Cretaceous are not artefacts of the edge effect.

1. Introduction

Signatures of catastrophic mass extinctions have long been suggested to be obscured by what is known as the “edge effect” [1–4] where taxonomic diversity appears to decline gradually towards mass extinction events when no such long-term declines actually occurred. Edge effects have been discussed by palaeontologists, and termed the Signor-Lipps Effect (SLE), after the empirical observation [1] that specimens are undercounted near key boundaries and a sudden event can appear to have been smeared back in time. The assumption has been that the SLE occurs because of artificial truncation of incompletely sampled range data. Empirical temporal ranges of fossil taxa are incomplete (you never find the first example of species X, nor the last example), but it is also necessary to sample before and after a time of interest in order to make a reasonable estimate of what was present within that time span. If collecting is truncated either before or after the time of interest, then inferred diversity is reduced artificially. The SLE has been presented in reference to mass extinctions, where species ranges are truncated by the mass extinction event, and so there is a risk of undercounting in the last time stage before the crisis, because there are no later occurrences of the extinction victims to compensate for rarity.

While, SLE has historically been considered in the context of species richness and abundance, recently, models of diversification based on splitting of branches (speciation events) on a phylogenetic tree have also been suggested to be affected, whereby divergences (nodes on a phylogeny) are under-sampled in lineages that are temporally proximal to the edge [5]. The rationale is that by leaving no descendant lineages beyond the mass extinction event, the probability of not sampling lineages and thereby speciation events increases towards the edge [5]. This translates to an artificial decrease in the probability of observing speciation events towards the edge and has been suggested as a possible mechanism for the observed diversification declines in phylogeny-based diversification models [5, 6].

However, while theoretically plausible, whether the number of nodes observed along the evolutionary histories of species temporally proximal to the edge are indeed lower than those from older time intervals has not been explicitly tested or empirically demonstrated. More crucially, it remains untested whether declines in diversification rates inferred from phylogenetic models of diversification are artefacts of undersampling owing to the edge effect. Additionally, although the SLE has been demonstrated at the level of specimens and range ends of individual species within individual rock sections and over thicknesses of tens of metres of rock, representing time spans of typically no more than tens of thousands of years, it is not clear that it is appropriate to scale up such deficits in specimens on short time spans to millions or tens of millions of years and to clade level, and in particular to sampling of phylogenetic nodes over macro-evolutionary time scales.

Here, we test whether the numbers of nodes along the evolutionary histories of each species on a phylogenetic tree of dinosaurs are significantly lower in species occurring in geological stages towards the end of the Cretaceous Period using a phylogenetic model framework [7]. Additionally, we also test whether a more broad-scale pattern of fossil sampling through time (i.e., number of fossil occurrences at each geological stage) better explains the distribution of nodes through time. It is possible that modelled diversification dynamics reflect patterns of fossil sampling irrespective of the edge effect – i.e., sampling of fossils may be progressively worse throughout the latter half of the dinosaurian fossil record.

Taken together, our aims are: (i) to determine whether the number of nodes from root to each tip (N_{Nodes}) is lower in species occurring towards the end of the Late Cretaceous (the edge effect); (ii) whether such an edge effect can better explain the diversification decline previously observed in the three major clades of dinosaurs [7]; and (iii) whether patterns of fossil sampling through time can explain the distribution of N_{Nodes} through time.

2. Material And Methods

(a) Testing SLE on N_{Nodes} in Late Cretaceous stages

We modelled potential effects associated with each geological stage of the Late Cretaceous (Cenomanian, Turonian, Coniacian, Santonian, Campanian, and Maastrichtian) as intercept offsets of binary (0|1) dummy variables. These offsets are tested against the global intercept, which is the phylogenetically corrected mean estimate for N_{Nodes} (β_0). A significant SLE would be associated with a negative regression coefficient (lower N_{Nodes} than average) in the terminal Maastrichtian stage, but also possibly in the Campanian stage [5]. However, as it is not clear just how far SLE can extend back in time, we tested whether we could detect SLE (or indeed any other stage-specific effects) in earlier stages of the Late Cretaceous (Cenomanian, Turonian, Coniacian, and Santonian) as well. In other words, we modelled separate effects for each of the six stages in the Late Cretaceous.

The dummy variables for each stage are 0|1 binary state variables where species coded 1 are those that have temporal ranges (between their first and last appearance dates, FAD and LAD respectively) that

overlap with the stage of interest. Since we are interested in whether the occurrence of a species in Late Cretaceous stages can explain declining diversification rates, we only coded these dummy variables for species in the three major clades (Ornithischia excluding ceratopsids and hadrosauriforms, Sauropodomorpha, and Theropoda) for which this time-dependent process has been observed previously [7].

We further accounted for differences in mean N_{Nodes} amongst the five dinosaurian subclades [7] (Ceratopsidae, Hadrosauriformes, Ornithischia (excluding ceratopsids and hadrosauriforms), Sauropodomorpha, and Theropoda), as additional intercept offsets (electronic supplementary material). Thus, the effects of stages on N_{Nodes} are those after variance in N_{Nodes} associated with group membership has been accounted for.

We determined whether a regression coefficient was significantly different from zero based on the proportion of the posterior distribution of each regression coefficient that bounded zero (p_{MCMC}), where $p_{\text{MCMC}} < 0.05$ equates to a significant difference. In other words, a posterior distribution is significantly different from zero if greater than 95% of the values are either greater than or less than zero.

We then removed stage-specific dummy variables that did not have significant effects (a backward elimination). We used the reduced set of variables for our final model comparisons and interpretations.

(b) SLE on time-dependent diversification processes

We fitted and compared three additional models in which different time-dependent diversification processes are incorporated into the above model framework: Model A) time-linear model ($N_{\text{Nodes}} = \text{Time}$); Model B (time-square root model, $N_{\text{Nodes}} = \sqrt{\text{Time}}$); and Model C (time-quadratic model, $N_{\text{Nodes}} = \text{Time} + \text{Time}^2$). As heterogeneous time-dependent diversification processes have been observed previously for the five subclades, we modelled these additional effects separately following Sakamoto et al. [7]; that is, only the effects of Time (and not $\sqrt{\text{Time}}$ or Time^2) were modelled for hadrosauriforms and ceratopsids in Models B and C.

If the previously observed diversification decline [7] is better explained by SLE than a time-quadratic process, then either Models A or B would be preferred over Model C through DIC (deviance information criterion) comparisons, when stage-specific effects are present in the models. Furthermore, Time^2 in Model C would be expected to lose its effect (i.e., cease to be significant).

(c) Time-varying SLE on time-dependent diversification processes

As SLE can be time-varying, whereby its effects are progressively larger towards the edge, we also modelled SLE as an interaction term with Time . To secure enough variation in time, we consolidated taxa in the last two stages as being those at the “edge” and modelled both intercept offsets and time-varying effects (a total of seven additional models, electronic supplementary material). We modelled the time-dependent processes as described above for taxa distributed in time from the root to the end of the

Santonian, but modelled time-varying SLE for the taxa in the last two stages. As preliminary analyses revealed that the $Time^2$ term will become impossible to estimate in the last two stages, we only modelled an interaction term between the edge variable and $Time$.

(d) Effects of incomplete fossil sampling on time-dependent diversification processes

To test whether N_{Nodes} is associated with a broader pattern of sampling throughout the Mesozoic (and not just SLE), we fitted a further four models where the stage-specific effects in the above models are replaced with the number of fossil occurrences (N_{Occ}) at each stage. We downloaded occurrence data from the Paleobiology Database (PBDB) [8] for the taxon “Dinosauria” during the Mesozoic Period. N_{Occ} is the number of occurrences that existed at any time during the temporal range of each species in our phylogenetic tree. More specifically, for each species in our phylogeny, we subset the PBDB occurrences to those that overlap with the species range and counted the number of occurrences in this subset. This approach differs from the parameterisation of the stage-level effects outlined above in that the estimated parameter is based on an ordinal explanatory variable rather than a 0|1 binary state, meaning that the estimated effect depends on the value of N_{Occ} rather than a simple descriptive coefficient of the average N_{Nodes} within each stage.

(e) Phylogenetic trees

We used the most recent and largest meta-tree of Dinosauria ($N = 960$) [9] available in the literature. We took a random sample of 100 meta-trees from the 1000 most parsimonious trees (MPTs) supplied by Lloyd et al. [9] and scaled the branches according to the first and last appearance dates (FAD and LAD, respectively) of the tips, using the “equal” approach available in the paleotree R package [10]. We used a root divergence date of 248.7 million years (Myr) ago, based on the median divergence estimate from Lloyd et al. [9]. We removed one species that had a temporal range spanning the Cretaceous-Paleogene (K-Pg) boundary.

(f) Model fitting and selection

The phylogenetic Poisson models were implemented as a generalised linear mixed model (GLMM) in the MCMCglmm R package [11] following Sakamoto et al. [7]. Each model was fitted on all 100 trees through Markov Chain Monte Carlo (MCMC) over 10^6 iterations, discarding the first 10^5 iterations as burn-in and sampling every 1000 iterations after convergence. See Sakamoto et al. [7] for priors. We selected the model that has a DIC value that is at least 4 less than the model with the next lowest DIC value [7, 12].

3. Results

(a) SLE on N_{Nodes}

We found that out of the six stage-specific effects we parameterised, only the last two stages of the Cretaceous Period, the Campanian and the Maastrichtian, were associated with posterior distributions of

estimated regression coefficients that were significantly different from zero (Fig. 1). The Campanian and Maastrichtian stages have significantly positive effects on N_{Nodes} (median coefficients are 0.07 and 0.08 respectively after removing stages with no significant effects; $p_{\text{MCMC}} < 0.05$ in 100% of the trees; electronic supplementary material), meaning that dinosaurs in the last two stages are associated with significantly higher N_{Nodes} than those in previous stages (Fig. 1), as well as at the root (the phylogenetically corrected mean estimate, β_0). The direction of this effect is opposite to what would be associated with SLE, suggesting that there is no negative SLE on N_{Nodes} , contrary to previous suggestions [6, 13]. Our results indicate that nodes are not under-sampled towards the K-Pg boundary and that they are in fact slightly better sampled compared to previous time intervals (Fig. 1).

Furthermore, the individual effects of the Campanian and Maastrichtian Stages are not significantly different from each other (Fig. 1; electronic supplementary material). There is no significant difference between N_{Nodes} between these two stages, meaning that there is no observable decline in N_{Nodes} from the Campanian to the Maastrichtian that can be attributed to SLE.

Table 1

Summary statistics of MCMCglmm runs over 100 trees.

Median values of the posterior distributions of each coefficient are shown along with the percent of the trees in which posterior distributions are significant at $p_{\text{MCMC}} < 0.05$.

Variable	Median Coefficient	Percent Significant
(Intercept)	1.039	100
Th	0.913	100
O	0.096	0
S	0.971	100
C	-1.114	0
H	1.424	100
<i>Time</i> :Th	0.018	100
<i>Time</i> :O	0.022	100
<i>Time</i> :S	0.019	100
<i>Time</i> :C	0.018	56
<i>Time</i> :H	0.006	100
<i>Time</i> ² :Th	-0.00006	100
<i>Time</i> ² :O	-0.00007	100
<i>Time</i> ² :S	-0.00006	100
Campanian	0.081	100
Maastrichtian	0.117	100
Data accessibility		
Data and codes are available at Dryad (Doi:)		

(b) SLE on time-dependent diversification processes

Model comparisons reveal that model fit improves with the addition of the time-dependent processes, Time , $\sqrt{\text{Time}}$ and Time^2 , with the time-quadratic model (with group-wise heterogeneous processes taken into account) being the best model by far (Fig. 2; electronic supplementary material; $\Delta\text{DIC} >> 4$ in favour of the time-quadratic model over the other three models). This means that even after accounting for stage-specific effects, the time-quadratic model still explains the distribution of N_{Nodes} through time better than the simple Time -linear and Time -square root models.

Furthermore, we did not detect any progressive changes in effect through time towards the edge – that is time-varying SLE when modelled as an interaction term between an *Edge* variable and *Time* is not significant (electronic supplementary material). This reflects our results from the stage-level intercept offsets where estimated coefficients are not significantly different between the Campanian and the Maastrichtian (Fig. 1).

Additionally, the $Time^2$ coefficient remains significant in the three major clades of dinosaurs for which this process was modelled (Table 1). After accounting for the sampling of nodes in the Campanian and Maastrichtian Stages, the inferred underlying time-dependent processes still show strong signatures of diversification declines in the three major clades of dinosaurs (Fig. 3).

(c) Effects of fossil sampling on time-dependent diversification processes

Model comparisons using DIC reveal that the inclusion of N_{Occ} instead of the stage-level effects for the last two stages does not generally improve model fit for the time-quadratic model (Fig. 2; electronic supplementary material). This indicates that the stage-level positive effects associated with the Campanian and Maastrichtian stages are consistent with that of N_{Occ} – the regression coefficient for N_{Occ} is small but positive ($4.7 \cdot 10^{-5}$; $p_{MCMC} < 0.05$ in 100% of the trees). N_{Occ} is highest in the Maastrichtian with that in the Campanian being on the higher end (electronic supplementary material). Thus, the effects of N_{Occ} are qualitatively identical to those of the Campanian and Maastrichtian when the latter are modelled as intercept offsets using 0|1 dummy variables.

The addition of time-dependent processes improved model fit, with the time-quadratic model (with group-wise heterogeneous processes taken into account) being the best model by far (electronic supplementary material; $\Delta DIC >> 4$ in favour of the time-quadratic model over the other three models), as was the case with the stage-specific dummy variables. The $Time^2$ effects remained significant in the presence of N_{Occ} . While there is evidence to indicate that N_{Nodes} increases with increasing N_{Occ} (positive effect), the fact that the $Time^2$ effect remains significant after accounting for the positive effects of N_{Occ} and that N_{Occ} is highest immediately before the K-Pg boundary, indicate that the observed diversification decline towards the K-Pg boundary is not an artefact of incomplete fossil sampling. N_{Nodes} is not under-sampled because of progressively incomplete N_{Occ} towards the edge – the evidence suggests the opposite (Figs. 1, 3).

4. Discussion

(a) Patterns of speciation events throughout the Late Cretaceous

Interestingly, although N_{Nodes} were higher than expected in the last two stages when compared to the root state or earlier stages of the Late Cretaceous (as modelled as intercept offsets), when time-dependent processes are included, then the effects are slightly negative in both *Time* and \sqrt{Time} models (electronic supplementary material). This means that when a constant rate of diversification through time is assumed (in both the *Time* and \sqrt{Time} models), the observed N_{Nodes} is lower than expected towards the

end of the Cretaceous. This lower-than-expected N_{Nodes} given constant-rate time-dependent processes, does not, however, imply that there is an under-sampling of nodes towards the end of the Cretaceous, but rather that constant-rate time-dependent diversification processes are poor descriptors of the distribution of N_{Nodes} through time. The Time^2 process models this pattern better (through DIC comparisons contra [13]) and even preserves the slight over-sampling effects of the last two stages, more reflective of the underlying data structure.

(b) Implications for diversification declines in dinosaurs

Contrary to arguments in favour of an asymptotic model of diversification in dinosaurs [13, 14] and that observed declines in diversification rates are artefacts of edge effects or incomplete fossil sampling [5, 6], our results do not support either claim. As we demonstrate above, nodes are not under-sampled proximally to the K-Pg boundary [5, 6] but they are in fact, well sampled (Fig. 1). After accounting for this slight over-sampling, we detect significant signals of diversification decline towards the K-Pg boundary (Fig. 3).

It is worth noting that while the time-square root model is used as a benchmark for an asymptote model of diversification (where the rate of N_{Nodes} accumulation slows down towards an asymptote) [7, 13], in practice the predicted values do not converge onto a net-zero diversification rate but instead on a constant net-positive rate (Fig. S1b, e). This means that the time-square root model does not represent a diversification process towards an asymptote, but instead a slower yet steady increase through time (Fig. S1b), only at a lower rate than the time-linear model (Fig. S1d, e). This is the primary reason why this model is consistently rejected in favour of the time-quadratic model (Figs. 3, S1c, f) – it fails to sufficiently model the slowdown in diversification rates (Fig. S1b).

Whether or not such modelled diversification declines can be interpreted as evidence that the dinosaur subclades were undergoing natural deflation before their final extinction 66 Myr ago is debatable. Our preferred interpretation is that the three major subclades of dinosaurs were merely diversifying at an ever-decreasing rate, considerably lower than expected for clades of their sizes and long evolutionary histories. There is no doubt that dinosaurs dominated the terrestrial ecosystems globally until they catastrophically went extinct at the K-Pg boundary; dinosaurs were hugely abundant and globally ubiquitous. A diversification decline in this context then implies that dinosaurs were nowhere near as diverse as would be expected given their long-standing dominance. This translates ecologically into a reduction in resilience whereby less diverse groups of assemblages make up the predominant faunal ecosystems (regardless of their dominance) [15] which are dependent on long-lasting environmental stability. Such ecosystems are then vulnerable to catastrophic disasters such as an asteroid impact .

Our finding that dinosaurs were not under-sampled in the Maastrichtian in comparison to the other Cretaceous stages, is supported by empirical palaeontological-geological data [16] and modelled preservation rates [17] but has previously been rejected by other empirical [18] and modelling [19] studies. Part of the confusion has arisen perhaps because analysts switch between global-scale and regional-

scale studies. In fact, the sampled fossil record of dinosaurs in North America through the Campanian and Maastrichtian provides a large part of the global signal, with some matching data from European sites, considerable data from Argentina and Mongolia, but with very uncertain dating, and virtually nothing from Africa, Australia and the rest of Asia [18, 20, 21]. Counts of dinosaur-bearing geological formations worldwide showed that numbers reached a peak in the Maastrichtian, implying excellent opportunities to sample [16, 22]. The high numbers of dinosaur localities, collections, formations, and skeletal quality in the Campanian and Maastrichtian were also noted as evidence for good sampling and the reality of the Late Cretaceous downturn in dinosaurian diversity dynamics [7]. Similar results emerged from modelling of dinosaurian preservation rates as part of a Bayesian study of speciation dynamics of North American dinosaurs [17]; preservation rates remained low (< 2 occurrences per lineage per million years) through much of the earlier Cretaceous, and then climbed to 4 in the Campanian and 7.5 in the Maastrichtian, so improving by > 400% from Santonian to Maastrichtian [17].

On the other hand, other authors argue that the latest Cretaceous was a time of poor sampling and that the apparent downturn in dinosaur diversity is an artefact [18, 19]. All the 'sampling metrics' used by Upchurch et al. (2011) [18] are closely correlated with each other and with dinosaurian diversity, with highs in all metrics in the latest Cretaceous; residuals of dinosaur diversity minus the geological metrics tend to flatten the face-value diversity curve because in fact the 'sampling metrics' are redundant with the diversity measures, and the meaning of the result is unclear [23]. Further, Chiarenza et al. [19] showed that the area of exposed rocks in the western United States representing habitats suitable for dinosaurs to occupy declined through the Campanian to Maastrichtian. However, using ecological niche modelling for the whole of North America, they showed that habitats suitable for dinosaurs remained constant or increased slightly through the Campanian and Maastrichtian, and so they argued that sampling was becoming worse through those two stages and that the decline in dinosaurian diversity [7] was an artefact of poor sampling. The ecological niche modelling approach [19] makes many assumptions, not least that it can define areas where dinosaurs are absent but ought to be found, and this could be disputed in view of the limited input variables used to define 'suitable' habitats. Further, it is not explained [19] how discovering the 'unsampled' dinosaurs would affect the continental-scale taxon counts.

Endemicity was not great in the Late Cretaceous, so the unsampled, or under sampled, dinosaurs of eastern North America would probably only add a few previously unknown species, but no new genera or new families. If the study was to estimate dinosaurian abundance or biomass, then missing fossils from such a wide area would substantially underestimate values, but if the target is biodiversity at species or genus level, it would likely make little difference, and certainly not to our phylogeny-based finding of a substantial decline in dinosaurian diversification rates over tens of millions of years. Phylogenetically, the addition of species from previously known Late Cretaceous families will not increase effective sample sizes. Adding another tyrannosaur or ankylosaur or ornithomimosaur, etc, will not drastically (or fundamentally) alter the picture of Late Cretaceous dinosaur diversity, but adding a hitherto unknown radiation of an entire clade or a hidden diversity of an ancient clade – e.g., basal theropods – might (both of which are highly unlikely for eastern North America). The majority view [7, 16, 17, 21, 22, 24, 25] is that

dinosaurs, in North America at least, were remarkably well sampled through the Campanian and Maastrichtian, and showed a decline in diversity and in speciation dynamics through this time.

Finally, as SLE has historically been discussed at the level of specimens within individual rock sections, it is predicated on the fact that the stratigraphic sequence is more or less complete. That is, whether a fossil occurrence is observed at a particular horizon depends on the probability of observing a fossil occurrence given the presence of rock. Then, this sampling probability (or sampling rate) often can be over longer time intervals (e.g., over one million years) than the depositional rate of the stratigraphic sequence. In such cases, sampling will decrease towards the edge as the probability of finding a fossil will diminish with less rock to search in [1, 4].

Dinosaur discoveries over their entire evolutionary history, on the other hand, are strongly correlated with rock availability [16, 18] – dinosaur discoveries even drive the discovery of new fossiliferous formations. Thus, on a macro-evolutionary time scale over 150 + Myrs, sampling rate and depositional rate are expected to be closely linked with each other, making the SLE unlikely to be a major influencer of diversification estimates. That is not to say however, that there are no sampling effects, as we do demonstrate that N_{Occ} is significant in our models and as dinosaur diversity is tightly correlated with the number of dinosaur-bearing formations [16, 18].

While there are many uncertainties surrounding diversification dynamics of extinct clades, what is clear is that our model of diversification does not appear to suffer from an artefact owing to the under-sampling of nodes close to the edge (i.e., SLE), but rather that there is sufficient sampling (even slight over-sampling) of nodes. Dinosaurs, except for hadrosauriforms and ceratopsids, were not diversifying as expected given their evolutionary history and sizes of their clades, with their diversification trajectories on a downward trend towards the K-Pg boundary.

Tables

Declarations

Data accessibility

Data and codes are available at Dryad (Doi:)

Competing interests

We declare we have no competing interests.

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Figures

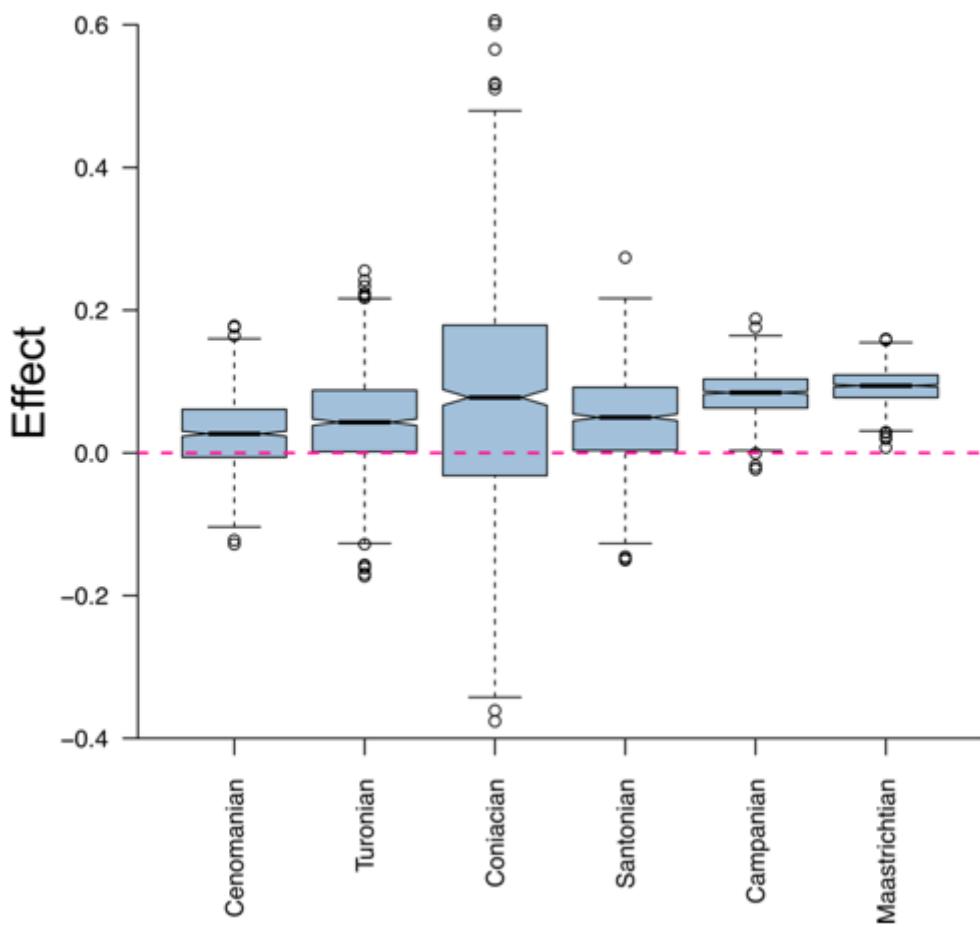


Figure 1

The effects of Cretaceous stages on NNodes. The posterior distributions of the estimated regression coefficients for each stage are shown as boxplots. These are offsets from the global intercept (phylogenetically corrected mean NNodes) and represent the effect of each stage on phylogenetically corrected NNodes. Significant effects are those where >95% of the posterior distribution lie on one side of zero (pink dashed line; Table 1). The last two stages of the Cretaceous Period, the Campanian and the Maastrichtian, are associated with small but significant positive effects when modelled in a phylogenetic framework, contrary to the postulated negative effects owing to SLE.

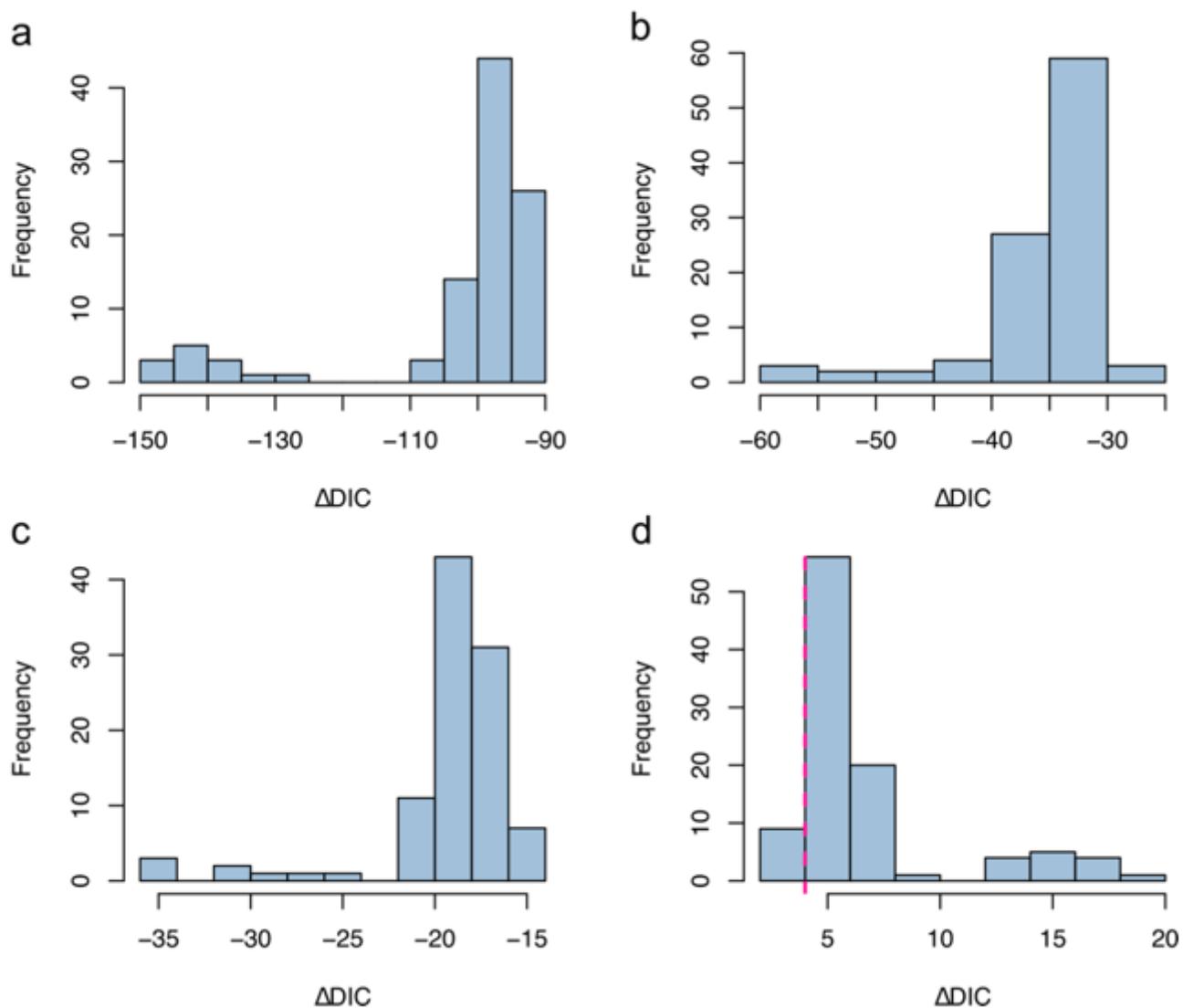


Figure 2

Model comparisons based on DIC. Models were compared using differences in DIC values (ΔDIC) between: (a) Time-quadratic model with stage-wise effects (last two stages) and the stage-wise offset model (last two stages); (b) Time-quadratic model with stage-wise effects (last two stages) and Time-linear model with stage-wise effects (last two stages); (c) Time-quadratic model with stage-wise effects (last two stages) and Time-square root model with stage-wise effects (last two stages); and (d) Time-quadratic model with stage-wise effects (last two stages) and Time-quadratic model with sampling effects (NOcc). Negative ΔDIC values indicate favourable fit for the Time-quadratic model with stage-wise effects (last two stages), while positive ΔDIC values indicate favourable fit for the alternative model. Pink dashed line shows the threshold value of $\Delta\text{DIC} = 4$. Replacing stage-wise effects with NOcc does not significantly improve model fit (d).

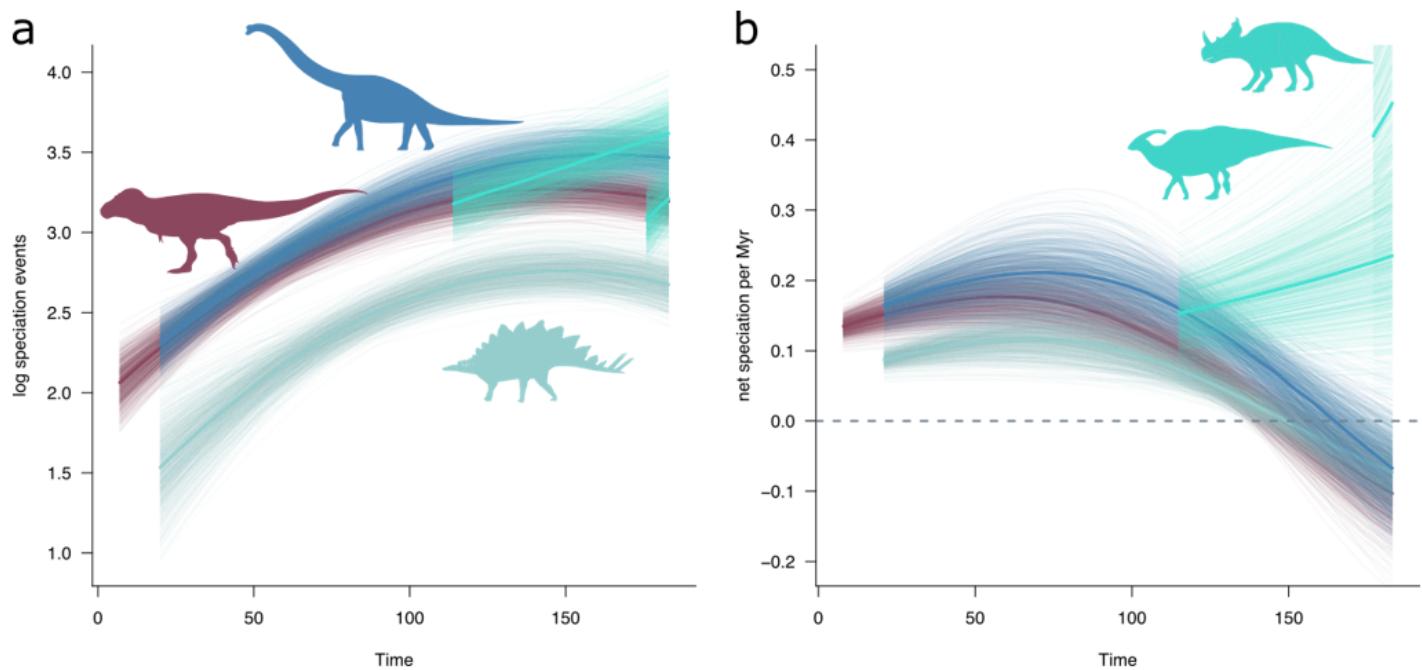


Figure 3

Number of speciation events predicted from the phylogenetic model of diversification through time and net speciation per Myr. Speciation events were predicted from the Time-quadratic model with SLE (stage-wise effects for the last two stages) (a). Net speciation per Myr (b) – or diversification rates – were calculated as the differences in predictions (a) at 1 Myr intervals. Note diversification rates are on a downward trajectory in the three main clades of dinosaurs even after accounting for the SLE. Silhouettes represent the five groups of dinosaurs for which separate coefficients were estimated: red, Theropoda; blue, Sauropodomorpha; green, Ornithischia (excluding Ceratopsidae and Hadrosauriformes, aqua). Silhouettes downloaded from PhyloPic.org and are by: Tyrannosaurus rex, Jack Mayer Wood (CC BY 3.0); Giraffatitan brancai, Mathew Wedel (CC BY 3.0); Stegosaurus, Andrew A. Farke (CC BY 3.0); Centrosaurus, Andrew A. Farke (CC BY 3.0); and Parasaurolophus walkeri, Jack Mayer Wood (Public Domain).

Supplementary Files

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- [TableS.xlsx](#)