Comment on "Impacts of the Cretaceous Terrestrial Revolution and KPg Extinction on Mammal Diversification"

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Meredith *et al*. (Reports, 28 October 2011, p. 521) question three findings of our delayed-rise hypothesis for present-day mammals made with reference to the Cretaceous-Paleogene (KPg) boundary, based on their new time tree of the group. We show that their own data do not support their objections and that the macroevolutionary patterns from the respective phylogenies are not statistically different.

Meredith *et al*. (*1*) present a complete family-level time tree of extant mammals through a molecular supermatrix analysis of exemplars of each taxonomic family. On the basis of this phylogeny, they criticize our findings from a nearly complete, dated species-level supertree of the group (*2*, *3*), indicating large differences in both topology and inferred temporal patterns of diversification between the respective sets of trees.

Surprisingly, Meredith *et al*.'s macroevolutionary analyses were not made using their supermatrix trees (like the exemplar in their figure 1). Instead, to avoid artifacts from an incomplete sampling of lineages originating before 40.4 million years ago (Ma) (the temporal limit of their analyses), they used a compartmentalized form of supertree construction—the very method they condemn in their supporting online material—to graft up to 10 lineages onto their supermatrix backbone trees. More importantly, despite the topological differences between the respective supertrees, the macroevolutionary differences from our study highlighted by Meredith *et al*. are either simply not present or not statistically significant: Their supertrees confirm, rather than conflict with, our proposed delayed-rise scenario for mammalian diversification.

First, while emphasizing a significant increase in net diversification before 78 Ma during the Cretaceous Terrestrial Revolution (KTR), Meredith *et al*. completely fail to mention that we reported a highly significant peak around this time in our paper (*2*).

Second, Meredith *et al*. themselves note that their analyses provide "no statistical support for a rate increase at or near the KPg boundary" (*1*). This again confirms our findings, but contradicts their own conclusion that their analyses suggest an important role for the Cretaceous-Paleogene (KPg) mass extinction in opening up ecospace to drive mammalian intraordinal diversification. We do not doubt this latter statement in general, but it has no support from their diversification analyses, and the question remains why the ancestors of extant mammals did not take greater advantage of the opportunity presented. Using an independent analysis of fossil occurrences, we hypothesized that now-extinct lineages of mammals filled up the newly available ecospace initially before being replaced by modern forms (*2*); Meredith *et al*. provide no equivalent explanation.

A reanalysis of all eight Meredith *et al*. supertrees with generalized additive models (GAMs) of net diversification through time—the method we used previously—reinforces the missing KPg peak: Net diversification rates are at best constant, but usually decreasing, through the boundary (Fig. 1). In this respect, GAMs are more flexible than the maximum likelihood birth-death shift method (*4*) used by Meredith *et al*. and do not require that all contemporaneous lineages had equal chances of diversifying [an unreasonable assumption for mammals (*5*)].

Third, Meredith *et al*. are wrong to claim that their analyses contradict our hypothesized post-Paleocene acceleration in net diversification. (Importantly, we did not claim, as they say we did, a "dramatic upturn in diversification rates in the Eocene ~55 to 50 million years ago.") GAMs show that net diversification rates are consistently decreasing to a low at 40.4 Ma in all their supertrees (Fig. 1), meaning they must have increased subsequently to have generated enough extant diversity. Rather than suggesting no delay after the boundary, their data indicate an even longer one than we reported.

Finally, unlike their birth-death shift method, our GAM approach can statistically compare the diversification dynamics embodied by two phylogenies, going beyond the qualitative comparisons of Meredith *et al*. to actually test the null hypothesis that the two trees reflect the same macroevolutionary regime. To test for pairwise differences among their eight and our three supertrees (*3*) from 129.0 to 40.4 Ma, we used a temporal grain of 0.1 million years (the precision of the node ages in our trees) and a gamma value of 1.4 [see (*6*)] and varied the basis dimension in the GAMs to maximize the number of significant pairwise differences. The optimal basis dimension (10) produced 11 significantly different pairs, none of which involved our "best-dates" supertree. Although an omnibus test would be more appropriate for testing the overall null hypothesis because of the multiple comparisons, the pairwise tests serve to make our main point: Our conclusions about the temporal pattern of diversification rates are not significantly different from those produced by any of Meredith *et al*.'s supertrees.

In conclusion, contrary to the impression promoted in their paper, Meredith *et al*.'s data broadly confirm our delayed-rise scenario for the temporal pattern of extant mammalian diversification: high rates well before the KPg boundary in the KTR; stable, lower rates across the boundary; and a subsequent rise in rate sometime after the Paleocene.

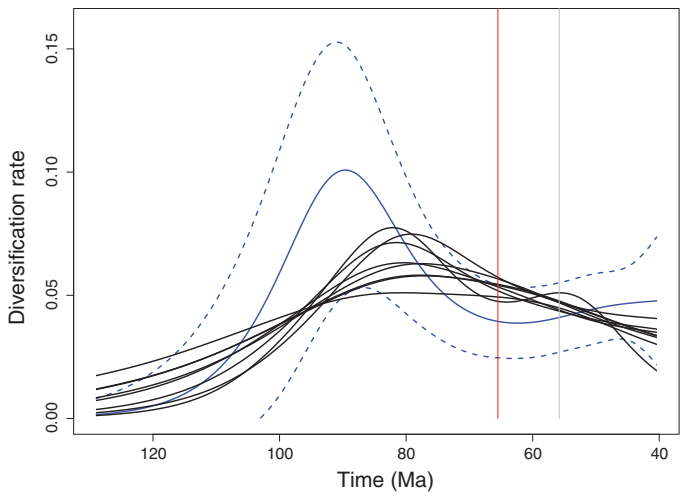

Fig. 1. Net diversification rates through time inferred from GAMs. Blue curve, rates from Bininda-Emonds *et al*.'s (*3*) preferred dates; dashed curves, 95% confidence intervals; black curves, rates from Meredith *et al*.'s eight supertrees. Red vertical line, KPg boundary (no trees indicate rates were rising at this time); gray vertical line, Paleocene-Eocene boundary.

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