**TITLE:**

No evidence, indeed: a critique of Thompson and Ramirez-Barahona (2023)

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**Abstract**

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**Introduction**

Since the introduction of molecular phylogenies and the comparative methods that employ them, practitioners have defied expectations of what was thought possible. For example, when Felsenstein (1985) famously introduced phylogenetic independent contrasts, reviewers were skeptical that there would ever be sufficient robust phylogenies for the method to prove useful (Huey et al. 2019). Many would argue that another example of this is estimation of extinction rates from phylogenies that are entirely extant; however, this issue is much stickier. Nee et al. (1994) demonstrated that extinction rates can be estimated, and mass extinction events can be inferred, from lineage-through-time (LTT) plots that only contain information about lineage “births.” However, estimation of extinction rates from phylogenies of extant taxa has proven controversial: Rabosky (2010) went so far as to argue that extinction rates should not even be estimated from molecular phylogenies, while others, such as Beaulieu and O’Meara (2015), have argued that reliable extinction estimates can be gleaned from phylogenies that are sufficiently large using sophisticated methods that incorporate things like rate heterogeneity. Most recently, Louca and Pennell (2020) demonstrated that evolutionary rates cannot be reliably inferred from LTTs, inspiring widespread doubt in the degree to which inferences from phylogenies are stretched.

However, optimism remains – perhaps too much optimism. Recently, Thompson and Ramírez-Barahona (2023) attempted to detect a signature of the Cretaceous-Paleogene mass extinction on two very large phylogenies of flowering plants. They failed to do so, arguing that this demonstrated the resilience of angiosperms, likely due to their rich adaptations. This finding was discussed in several popular science articles, including in the New York Times. However, their paper contains two issues. The first is that this finding disagrees with several robust analyses of the angiosperm fossil record that display evidence of plants having undergone widespread extinction after the Cretaceous-Paleogene boundary (Labandeira et al. 2002; Wilf and Johnson 2004). While disagreeing with previous evidence is not necessarily an indication of an incorrect result, especially since the fossil record is imperfect, the fact that Thompson and Ramirez-Barahona have offered an answer to a paleobotanical problem using extant-only data can reasonably raise suspicion.

This reply investigates the aspects underlying the second issue with their study: overextending the capabilities of analyses of molecular phylogenies. Despite a veritable pile of papers sounding the alarm about limitations of phylogenetic comparative methods (both warranted and unwarranted), they continue to be applied to problems for which they can offer but limited information and ultimately produce suspect results. Here, we argue that the methods employed by Thompson and Ramirez-Barahona (2023) cannot confidently support the conclusion that flowering plants were not subjected to the ravages of the end-Cretaceous extinction. Specifically, we discuss the lack of phylogenetic information deep in the tree as well as high rates of model misspecification with the TESS model, and we conclude with an investigation of how including fossil taxa on phylogenies can potentially improve diversification studies.

**Lack of Information**

The supposed ability of Thompson and Ramirez-Barahona to reconstruct the severity of the Cretaceous-Paleogene extinction event on flowering plants from extant species alone relies on the fact that signatures of diversification rate heterogeneity are often retained by LTTs. Nee et al. (1994) note in their seminal paper on the subject that, in all their examples, they assumed 100% sampling, which the phylogenies used by Thompson and Ramirez-Barahona do not have. Another issue not discussed by Nee et al. (1994) is the fact that the evolutionary patterns gleaned from analyses of molecular phylogenies as opposed to those of the fossil record can often differ widely (Marshall 2017). This should not be particularly surprising given the fact that a very small proportion of organisms throughout geologic time are successfully buried and fossilized, preserved to the present, and ultimately excavated by humans (Foote and Miller 2007), as well as the fact that many evolutionary avenues, even ones that produce large clades over time, may ultimately leave no survivors to the present that can be included in molecular phylogenies.

But let’s assume, for the sake of argument, that the tree is roughly accurate in its representation of evolutionary patterns taken by the clade(s) represented, and that it represents all or nearly all of the extant species recognized by taxonomists. If this is the case for the phylogenies used by Thompson and Ramirez-Barahona (a proposition for which they provide no evidence, mind you), then they should be able to accurately infer signatures of past mass extinctions at any time along the LTT, right? Not necessarily. As one travels from the tips toward the root of a phylogeny, whether one is performing an ancestral state reconstruction or a diversification study or any other type of phylogenetic comparative analysis, the amount of information available to an investigator deteriorates. O’Meara and Beaulieu (2021) demonstrate this on a simulated tree with one million tips, arguing that analyses and inferences of evolutionary events deep on phylogenetic trees rely on the few lineages that survived to the present and were thus able to be sequenced and included in a molecular phylogeny. This may be a completely unrepresentative example with little information about the evolutionary events that shaped their clade and more inclusive clades in which they are nested.

In the case of Thompson and Ramirez-Barahona (2023), in one of the phylogenies they analyzed, produced by Smith and Brown (2018), only about 0.7% of all evolutionary events (speciations) in the Smith & Brown tree occur at or before 65 mya. Examined in another way, there are only 548 lineages present at the 65 mya timeslice, compared to about 77,000 tips in the Smith & Brown tree. While Thompson and Ramirez-Barahona (2023) do include in their discussion an admission of the potential lack of identifiability in any analysis of diversification deep in time, they were not dissuaded from performing (or publishing) their dubious analysis. These facts have spurred other scientists to develop and increasingly employ tip rate analyses (e.g., Title and Rabosky 2019; Vasconcelos et al. 2022) that take advantage of the glut of information available near the present, but which unfortunately are unable (at least at this point in time) to provide information about past mass extinction events in the distant past, and thus do not form a viable alternative for analyses like that of Thompson and Ramirez-Barahona (2023). O’Meara and Beaulieu (2021) do not provide optimism that such analyses may be viable in the future, and they instead advise biologists that “it is important to recognize that *our methods are better suited for using the past to learn about the present survivors, not using the present survivors to learn about the past*” (p. 21; emphasis in the original).

* Losos address (2011)
* How much information in Smith & Brown tree at time period of interest? (O’Meara and Beaulieu 2021)
* We are attempting to study something deep in the past “from a study of their weird, few surviving lineages” (O’Meara and Beaulieu 2021).
* There’s also uncertainty in the form of information loss (Boyko and Beaulieu 2021)

**TESS Issues**

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-High Type II error rate (SOURCE?)

-Our own analysis

\*Generate trees with various issues to stress-test

\*Models we run TESS with are constant BD, episodic BD, and mass ext

\*Extinct\_removed: Episodic supported over constant or mass ext

\*Mass ext sim tree: Episodic supported over constant or mass ext

**How Many Fossils Do We Need?**

The

-LTT plots can show very different results when a hypothetical tree has extinct taxa removed (like a normal one for a molecular phylogeny) vs. when extinct taxa are retained (Marshall 2017)

-Sepkoski (1975) suggests that survivorship curves [is this relevant?] can be accurate with just 20% of fossils discovered

-We stress-tested TESS by gradually removing extinct taxa from the phylogeny to see model results would change

**Conclusions**

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