

# Diversification rates, clade ages, and macroevolutionary methods

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Hena Diaz et al. (1), hereafter HDEA, claim to find a “hidden generality” about macroevolutionary rates, specifically, that diversification rates are faster in younger clades. However, this pattern was far from hidden. It was previously shown across the tree of life in a paper (2) cited by HDEA, but with no mention of the extensive overlap in their findings. For example, we (2) showed that “Diversification rates were negatively related to clade ages across the tree (kingdom:  $r^2 = 0.90$ ; phylum:  $r^2 = 0.19$ ; class:  $r^2 = 0.33$ ; order:  $r^2 = 0.07$ ; family:  $r^2 = 0.15$ ;  $p < 0.01$  in all cases).” This negative relationship was also found (at one or more taxonomic levels) within bacteria, protists, fungi, plants, and animals (2). Furthermore, HDEA do not study the “tree of life” as claimed. They include only plants and animals. In contrast, we included all major groups, including those they ignore (i.e., fungi, protists, bacteria, archaeans). Their study (1) includes 104 clades. Ours included >2,500 nonoverlapping clades. No extant clades in their study are >350 million years old or include >4,200 species. Ours included a clade >4 billion years old and another with >1.5 million species.

Although we agree with HDEA (1) that diversification rates are often faster in younger clades, we disagree with their primary conclusion from this pattern. They state, “First, this implies that it is not informative to use constant-rate estimators to compare diversification rates of clades of different ages” and that “our results provide a particularly clear demonstration that the constant-rate approach is inherently problematic.” They refer specifically to our (2) use of the method-of-moments estimator

(3). Strangely, they provide no evidence that this method gives problematic estimates when rates are faster in younger clades. However, that possibility was specifically addressed with simulations (4), which showed that strongly negative age–rate relationships did not significantly impact the accuracy of this estimator. That study (4) also showed that the “hidden” pattern “discovered” by HDEA was present across animal phyla and insect orders (i.e., most described species on Earth). Moreover, contrary to the unsupported claims made by HDEA, additional simulations (5, 6) showed that this estimator (3) can be accurate when rates vary dramatically over time within clades and when rates differ strongly among a clade’s subclades. None of these simulation studies are cited by HDEA. Overall, we think that the accuracy of macroevolutionary methods should be evaluated with rigorous simulations, not unsupported aspersions. The idea that the method-of-moments estimator (3) will necessarily give inaccurate results when rates vary within or between clades was already disproven before HDEA was published. Despite their conclusion, their study does not actually address this method’s accuracy, nor did the papers they cited as support.

Ironically, simulations show that the method (7) used by HDEA (1) performs increasingly poorly with increasing rate heterogeneity (6, 7). Furthermore, it can fail to estimate changing extinction rates within clades over time, instead assuming that changes in diversification rates over time within clades are caused only by changing speciation rates (8). These problems are not mentioned by HDEA, despite their obvious relevance.

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The authors declare no competing interest.

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