

PROBLEMS WITH MEASURING TAXIC, MORPHOLOGICAL, AND MOLECULAR RATES OF EVOLUTION: A METHODOLOGICAL OVERVIEW

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Estimating rates of evolution, whether taxic, morphological, or molecular, entails numerous conceptual and methodological difficulties. Some of these may be ontological: (1) because assigning rank to supraspecific taxa, even within a cladistic framework, is never entirely objective, rates based on enumeration of taxa of a given rank are questionable because the entities being counted are not likely to be comparable in any theoretically meaningful sense, (2) rates of character-state change assume those changes can be enumerated unitarily, but in what sense is a character-state transformation of one character "equal" to that of another character? (3) rates of character change within a species, or among species, presupposes that "species" have been individuated correctly and comparably, yet in the paleontological record at least, only character-state information is available to individuate those taxa: different concepts of species imply rates may be measured differently.

Difficulties in estimating rates may also be methodological. Rates of character change are sometimes estimated by transforming intertaxon differences/similarities to distances and then fitting them to a tree topology. Such transformations have the potential for error if distances are not corrected for homoplasy. With molecular data, these corrections necessitate assumptions, or empirical estimates, of patterns of character-state change (such as variation in probabilities of transition versus transversion substitutions) yet those parameters are themselves generally dependent upon some assumptions of relationships. Moreover, the values of those parameters will often vary depending upon the divergence times of the taxa being studied because of the accumulation of homoplasy.

While rates of character change are seemingly best studied by optimizing those changes directly on a tree, many factors can influence estimates of relative rates along each branch: (1) for a given set of taxa, there may be multiple equally parsimonious trees, each with different topologies and with different patterns of character optimizations, (2) even if there is a single most parsimonious tree, characters can be optimized in different ways, thus changing measures of rates, (3) different outgroups can change optimizations (and relationships of the ingroup) and thus lead to differences in rate estimation, and (4) adding or subtracting taxa (the taxic sample) can often alter patterns of optimizations and thus estimates of relative rate; thus assumptions about the extent of extinction within the group being studied are directly relevant for any determination of rates of change along branches leading to the taxa included in the sample.

Estimation of absolute rates presents additional difficulties because patterns of change within or across taxa must be calibrated to time. Rates depend upon assigning ages to lineages and the taxa being counted. Outside a cladistic framework accurate assignment is questionable, but even within a cladistic framework it is not at all straightforward.

None of these difficulties are arguments against efforts to measure rates of change, but to one degree or another they will have effects on the accuracy of our estimates and thus may need to be considered in any given analysis.