



Including the Characters of Interest During Tree Reconstruction and the Problems of Circularity and Bias in Studies of Character Evolution

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NOTES AND COMMENTS

INCLUDING THE CHARACTERS OF INTEREST DURING TREE RECONSTRUCTION AND THE PROBLEMS OF CIRCULARITY AND BIAS IN STUDIES OF CHARACTER EVOLUTION

Recent developments have clarified the critical importance of conducting comparative evolutionary studies in the context of phylogeny (e.g., Eldredge and Cracraft 1980; Felsenstein 1985; O'Hara 1988; Funk and Brooks 1990; Harvey et al. 1995), and this approach has been applied widely in studies of character evolution (e.g., Donoghue 1989; Brooks and McLennan 1991; Harvey and Pagel 1991; Martins and Garland 1991; Maddison and Maddison 1992; Eggleton and Vane-Wright 1994). Within this general phylogenetic frame of reference, a widespread belief has arisen that analyzing the evolution of particular characters in the context of phylogenetic trees based wholly or partly on those same characters is logically circular, and that independent phylogenies (i.e., ones based on data other than the characters under investigation) are needed to analyze character evolution properly (e.g., Coddington 1988; Carpenter 1989; Lauder and Liem 1989; Olmstead 1989; Sytsma 1990; Brooks and McLennan 1991; McKey 1991; Vane-Wright et al. 1992).

Here I critically analyze the logic of studying character evolution in a phylogenetic context, focusing on the practice of including the characters of interest during tree reconstruction as it relates to the problem of fallacious reasoning. I develop a position implicit in several earlier articles (e.g., Maddison 1990; Harvey and Purvis 1991; Armbruster 1992, 1993; Maddison and Maddison 1992; Swofford and Maddison 1992; Deleporte 1993; de Queiroz and Wimberger 1993) in which the existence of questionable logic is recognized as being dependent on the nature of the relationship between specific premises and conclusions or, more precisely, on how the assumptions inherent in specific methods or practices bear on specific hypotheses or inferences. I argue that both including and excluding the characters of interest can lead to logical problems, which implies that, although there is a valid concern about including the characters of interest during tree reconstruction, this concern cannot be eliminated by a simple rule to always exclude those characters. Finally, I make some general recommendations intended to promote increased rigor in analyses of character evolution.

DIFFERENT GENERAL PERSPECTIVES

The issue of fallacious reasoning in studies of character evolution is complicated by the existence of a larger controversy over whether it is generally preferable to include or exclude certain characters when reconstructing phylogenetic trees. The complication is that although the recommendations about what to do with the characters are in direct opposition—exclude versus include—the underlying reasons are not. Authors who favor excluding the characters of interest implicitly adopt a perspective that emphasizes reliability (in the sense of being cautious or conservative). They argue that the best inferences about character evolution must exclude the characters of interest from the data used to reconstruct the tree, because to include those characters results in circularity (see references above). The implication is that including the characters of interest predisposes an analysis to favor a particular outcome, which presumably leads to questionable inferences. In contrast, authors who favor including the characters of interest implicitly adopt a perspective that emphasizes accuracy (in the sense of being the single estimate that has the highest probability of being correct). They argue that the best inferences about character evolution must be based on the most accurate reconstructions of phylogeny, which must in turn be based on all of the available evidence, that is, including the characters of interest (e.g., Kluge 1989; Donoghue and Sanderson 1992; Maddison and Maddison 1992; Swofford and Maddison 1992; Deleporte 1993; de Queiroz and Wimberger 1993; McKittrick 1993). There are thus three different issues that would have to be addressed to resolve this larger controversy: how to maximize reliability, how to maximize accuracy, and the relationship between these two concerns. I will address only the first of these issues in detail, but I wish to comment briefly on the third because it clarifies the basis of the controversy and provides background for my analysis.

Although emphasizing either reliability or accuracy leads workers to opposite conclusions about whether to include or exclude the characters of interest, the general perspectives manifested in these different emphases are complementary rather than contradictory. The most accurate inferences about character evolution may well be based on the most accurate estimates of phylogeny, which may in turn be based on data that includes the characters of interest. But the most accurate inferences about character evolution (or anything else) are not necessarily the most reliable, and the most reliable inferences about character evolution are not necessarily based on the most accurate estimates of phylogeny. A tree that deviates from the most accurate estimate of phylogeny in a predetermined way can sometimes serve as the basis for a more reliable inference about character evolution. To the extent that excluding the characters of interest results in a tree that predisposes an analysis to favor an outcome that is cautious or conservative with respect to a particular inference—and including them predisposes it to favor an outcome that is not—the more reliable inference will be based on the analysis that excludes the characters of interest. This conclusion contrasts strongly with one that might be reached from the perspective that emphasizes

accuracy over reliability, according to which it may be appropriate to include the characters of interest regardless of (or, in that context, because of) their potential influence on the results. Given that the information in the characters of interest is not predominantly misleading, those characters provide evidence about the phylogenetic relationships of the taxa in which they occur and thus also about their own evolution. In any case, there is no reason to question the validity of either general perspective; both reliability and accuracy are legitimate concerns. Nevertheless, I will restrict the remainder of my discussion to the general perspective that emphasizes reliability, because this is the context within which the concepts of circular reasoning and problematic biases (see below) are most applicable.

LOGICAL FALLACIES AND OTHER PROBLEMS OF VALID INFERENCE

The practice of including the characters of interest in tree reconstruction is commonly characterized as an example of circularity or at least potential circularity (e.g., Felsenstein 1985; Coddington 1988; Olmstead 1989; Sytsma 1990; McKey 1991; Armbruster 1992; Donoghue and Sanderson 1992; Vane-Wright et al. 1992; de Queiroz and Wimberger 1993; Sillén-Tullberg and Møller 1993; Block and Finnerty 1994; Meyer et al. 1994), implying the logical fallacy known as arguing or reasoning in a circle. The *Oxford English Dictionary* (1989) defines “to reason or argue in a circle” (also “vicious circle argument” or “circular argument”) as an invalid form of argument in which a proposition is used to establish a conclusion, and afterward the proposition is justified by means of the very conclusion that it was previously used to establish. (The term *circular* in this context derives from the fact that, as in a circle, the argument has no clear starting point.) An example from evolutionary biology would be using a tree reconstruction method that minimizes instances of homoplasy (i.e., parsimony or minimum-evolution methods), concluding from its results that homoplasy is rare, and then using the conclusion that homoplasy is rare to justify use of the method that minimizes it.

Characterizing as circular the practice (proposition) of including the characters of interest as part of the data used to estimate the branching topologies of phylogenetic trees is misleading. In this case, a circular argument would be one in which a conclusion reached in an analysis that included the characters of interest was then used to justify the very practice of including those characters. This is not, however, the kind of argument with which evolutionary biologists have been concerned. Authors attempting to avoid supposed circularity in studies of character evolution have been concerned with the practice of including the characters of interest itself rather than with arguments or justifications for adopting this practice. That is, they have been concerned only with the validity of using a particular practice to arrive at a result rather than with the full circle that also uses the result to justify the original practice. Strictly speaking, this is not arguing in a circle (see also Maddison and Maddison 1992; Swofford and Maddison 1992).

A related fallacy, termed “begging the question” (also “*petitio principii*”), is

more relevant in that it bears on the logic of establishing conclusions rather than on that of justifying initial propositions. To beg the question is to take for granted the matter in dispute—in other words, to assume the conclusion in the premises of the argument. Although this fallacy is of limited applicability for scientists (as opposed to logicians) in that the premises must fully assume the conclusion, it is nevertheless related conceptually to other logically questionable arguments and analyses in which the premises exert an undesirable influence on the conclusions without fully assuming them. Scientists use the term *bias* for systematic errors, errors that are nonrandom and thus tend to favor particular outcomes or results. If the result favored by a biased method is the same one obtained in an analysis using that method, then a logical problem arises—namely, that ambiguity exists as to whether the result is supported by the data themselves as opposed to being an artifact of the methodological bias. I will call this problem “inappropriately biasing the analysis.” The example used above to illustrate the fallacy of circular reasoning includes an example of (but is not the same as) such an inappropriate bias. Given that the results of an analysis support the hypothesis that homoplasy is rare, use of tree reconstruction methods based on parsimony constitutes an inappropriate bias. Although these methods do not preclude the possibility of obtaining results in which homoplasy is common (Farris 1983), they minimize and thus systematically underestimate homoplasy, which biases the analysis in favor of the hypothesis that homoplasy is rare. Begging the question is the most extreme version of this problem in that the method in question makes a particular result inevitable rather than merely tending to favor it.

Not all biases are logically problematic. Biases that tend to favor a specific hypothesis are problematic if that hypothesis is supported by the results of an analysis containing the bias in question, but an identical bias is unproblematic—perhaps even desirable—if the same hypothesis is contradicted by the results. If the bias associated with a particular method or practice favors a different hypothesis than the one supported by the results, then those results are not attributable to the methodological bias, and the problem of ambiguity associated with biases favoring the supported hypothesis (see above) does not exist. For example, it would not be logically problematic to use a tree reconstruction method that minimizes homoplasy in an analysis in which the results supported the hypothesis that homoplasy is common. Because the methods minimize estimates of homoplasy, they bias the results not in favor of but rather against that hypothesis. The bias in such a case might be considered appropriate given the results. The concepts of appropriate and inappropriate biases are thus closely related to the concepts of conservative and liberal tests. An appropriate bias renders a test more conservative, whereas an inappropriate bias renders the test more liberal. A given bias can also be unproblematic if it is neutral with respect to the particular hypotheses being evaluated. If a bias does not favor any of the hypotheses under consideration, then it does not lead to inferential ambiguity regardless of which hypothesis is supported by the results. For example, it would not be problematic to use trees reconstructed using parsimony methods to analyze whether rates of evolution have been constant or variable among lineages. Insofar as these methods

bias the results in terms of the frequency of homoplasy rather than the distribution of character transformations among lineages, they do not bias the results in favor of either constant or variable rates.

The classification of a given bias as appropriate, inappropriate, or neutral depends on how that bias bears on the outcome of an analysis with respect to the hypothesis under consideration. Because the status of a given bias is specific to the particular hypothesis being evaluated, the same bias can be appropriate in one situation, neutral in another, and inappropriate in yet another. Moreover, when an analysis is exploratory in the sense of simultaneously evaluating two or more alternative hypotheses (rather than being designed specifically as an attempt to reject one of them), and when the hypotheses being evaluated are strict alternatives (so that contradiction of one implies support for the other and vice versa), then the classification of a given bias as appropriate versus inappropriate depends on the outcome of the analysis. In such a situation, the bias associated with a particular method or practice cannot be categorized as appropriate, inappropriate, or neutral until after the analysis has been conducted.

BIASES ASSOCIATED WITH INCLUDING (AND EXCLUDING) THE CHARACTERS OF INTEREST

The mere decision to include particular characters will rarely assume the precise result that is ultimately obtained concerning the evolution of those characters (though such an assumption is at least possible in the extreme case in which the character of interest is the only datum used to reconstruct the phylogenetic tree). On the other hand, this practice is expected to lead commonly to inappropriate biases, at least in some kinds of analyses. Of special concern are studies that seek to assess whether the distribution of a character among species is the result of single versus multiple evolutionary origins. In such studies, including the character of interest can be expected to bias the results in favor of single origins, particularly when parsimony methods are used to reconstruct the phylogenetic tree. Because parsimony methods minimize total homoplasy, including the characters of interest will tend to give results in which the numbers of their own reconstructed origins and losses are reduced relative to reconstructions on trees on which those characters had no influence (Maddison 1990; Maddison and Maddison 1992; Swofford and Maddison 1992). Such reductions will be logically problematic if the results support the hypothesis of a single origin.

Nevertheless, including the characters of interest does not lead to a logical problem if the results support multiple origins. Because the bias introduced by this practice will tend to favor a single origin, a result indicating multiple origins is not called into question by that bias. In this case, the bias associated with including the characters of interest is appropriate. For similar reasons, excluding the characters of interest will lead to logical problems if the results favor multiple origins, but it will not lead to logical problems if the results favor single origins. Thus, at least with respect to the question of single versus multiple origins, both including and excluding the characters of interest can be said to bias the results in that either practice will influence those results in a particular direction.

Whether the bias is appropriate or inappropriate, however, depends on which hypothesis is supported.

In other cases, including the characters of interest can result in a bias, but for a different reason. For example, in studies investigating the potential correlated evolution of two characters (Felsenstein 1985; Maddison 1990; Pagel 1994), including the characters of interest will tend to reduce the number of gains and losses in those characters—at least under parsimony methods—relative to optimizing them on a tree on which they had no influence (Maddison 1990). Therefore, including the characters of interest will likely render the test more conservative because with fewer changes it will be more difficult to obtain a significant correlation (Maddison 1990), and, conversely, excluding the characters of interest will likely render the test more liberal. It should be noted that the bias in this case merely affects the number of observations, rather than specifically favoring a correlation between the characters or the lack thereof. Furthermore, including the characters of interest—rather than excluding them—results in a more conservative test.

In still other cases, neither including nor excluding the characters of interest results in a significant bias. Consider an analysis of constant versus variable rates of evolution among lineages for a particular set of characters. Although reconstructing the phylogeny by either including or excluding the characters of interest may influence the numbers of inferred changes in those characters, neither practice is expected to predispose the analysis either to distribute the changes equally over branches of equal temporal duration or to concentrate them in one or a few such branches. Therefore, provided that the methods of tree reconstruction and character optimization do not contain inherent rate biases, the characters of interest can be optimized either on a tree derived from an entirely different set of characters or on one based entirely on the characters of interest without biasing the results in favor of either constant or variable rates.

RECOMMENDATIONS AND CONCLUSIONS

The examples offered here illustrate that reliable inferences about character evolution depend critically on how the assumptions or biases inherent in particular methods or practices bear on the specific hypotheses being evaluated. More specifically, they reveal that including the characters of interest as part of the data used to reconstruct a phylogenetic tree constitutes an inappropriate bias in some cases but not in others; that excluding the characters of interest also constitutes an inappropriate bias in some cases but not in others; and that in still other cases, neither practice constitutes a significant bias. For these reasons, logical problems cannot be avoided by adopting a simple rule to always exclude (or include) the characters of interest. Sound inferences are best accomplished by carefully considering how both practices are expected to influence the results of a given analysis and how those influences bear on the evaluation of the specific hypotheses under consideration. Nevertheless, one practice that can be discouraged is excluding entire sets of characters for the simple reason that they include the characters of interest as one or a few of their members. For example, some

authors wish to exclude all morphological characters simply because the characters of interest happen to be morphological (e.g., Block and Finnerty 1994; Meyer et al. 1994). Although a researcher may sometimes be justified in excluding the characters of interest to avoid a problematic bias, it is not justifiable to exclude other characters on the basis of their sharing some property with the characters of interest that is irrelevant with respect to the hypothesis or inference in question.

The appropriateness of excluding certain potentially informative characters from the process of tree reconstruction, even if only in some cases, suggests the need to reconstruct trees for the express purpose of evaluating specific hypotheses about character evolution. Sometimes a distinction is made between systematics, the discipline concerned primarily with reconstructing or estimating phylogenetic trees, and comparative biology, the discipline concerned primarily with using those reconstructed trees to study character evolution. Although this characterization is useful in describing different research emphases, it is also oversimplified. Comparative biologists cannot afford to limit themselves to using trees generated by systematists; they need to be actively involved in tree reconstruction. Regardless of whether they collect their own systematic data, comparative biologists benefit greatly from being versed in the analysis of such data—or, alternatively, from working closely with systematists—because it enables them to generate trees to meet their own needs (e.g., Losos 1994). It allows them to investigate, for example, the effects of both including and excluding characters (e.g., Armbruster 1993; Ronquist 1994) or to compare, under simultaneous optimization of the tree and the character of interest, the optimality of trees when the character is unconstrained with those for which the character is fixed at a value corresponding with the null hypothesis (e.g., Felsenstein 1985; Pagel 1994). Generating trees for the express purpose of evaluating specific hypotheses should promote not only more rigorous analyses and more reliable conclusions about character evolution but also a more thorough integration of systematics and comparative biology.

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