Syst. Biol. 47(3): 497–508, 1998

Properties of Matrix Representation with Parsimony Analyses

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Baum (1992) and Ragan (1992b) independently devised a method that uses additive binary coding and parsimony to combine trees derived from different data sets, a procedure Ragan termed matrix representation with parsimony analysis (MRP). Because the method utilizes the topology of source trees rather than the original data, (1) trees derived from different data types (e.g., molecular sequences, morphological characters, pairwise distances) and analyzed by different clustering techniques (e.g., maximum parsimony, maximum likelihood, neighbor joining) can be combined, and (2) the source patterns are evaluated on a more-or-less equal basis, so that the phylogenetic signal from data matrices with a smaller number of characters is not swamped by those with a larger number (see Miyamoto, 1985; Hillis, 1987). The method is also unusual in that (1) trees with different terminal taxa can be combined, a feature that among consensus methods characterizes only the supertree method (Gordon, 1986; Steel, 1992) and the modified semistrict algorithm of Lanyon (1993), and (2) it is less sensitive to conflict among source trees than are most conventional consensus techniques so that resolution is not necessarily lost as increasing numbers of conflicting trees are analyzed (see also Purvis, 1995b).

Although the appropriateness of MRP to phylogenetic inference has been discussed (Baum and Ragan, 1993; Rodrigo, 1993, 1996; Bruneau et al., 1995) and modifications to the method have been proposed (e.g., Purvis, 1995b; Ronquist, 1996), its properties, mechanics, and biases have not been considered in sufficient depth. We discuss some of the properties of MRP, show how MRP differs from standard consensus techniques, and explore some modifications to the method. Although other clustering methods, such as compatibility (Ragan, 1992a; Purvis, 1995b; Rodrigo, 1996), have also been suggested as methods for generating composite trees by using matrix representation, we will not discuss them.

THE BASIC PROCEDURE AND SUGGESTED MODIFICATIONS

MRP uses additive binary coding (Farris et al., 1970) to represent the hierarchical structure of trees as a series of "matrix elements" (Baum and Ragan, 1993:637). Each node (i.e., component; sensu Wilkinson, 1994) on each source tree is represented by a binary matrix element, with terminal taxa in the clade delimited by that node scored as 1 and all other taxa scored as 0. Taxa that are missing from an individual source tree are coded as missing for elements that represent that tree. Trees are rooted either by an all-zero outgroup (Ragan, 1992b; Purvis, 1995b) or by using a taxon common to all source trees (Baum, 1992). Parsimony analysis of the element matrix produces a tree or trees (hereinafter, the composite tree[s]; Purvis, 1995a) that most parsimoniously synthesize(s) the hierarchical information in the source trees (for details, see Baum, 1992; Ragan, 1992b). Analyses that generate multiple most-parsimonious composite trees (MPCTs) are summarized by using strict consensus to generate a consensus composite tree (CCT).

Purvis (1995b) argued that the topology of particular source trees can unduly influence that of the composite tree (Fig. 1). He attributed this to the lack of independence among elements derived from a source tree, which adds redundant information to the matrix. He removed this apparent redundancy by coding taxa that are in neither the clade delimited by the node nor its sister taxon as ? rather than 0. As with

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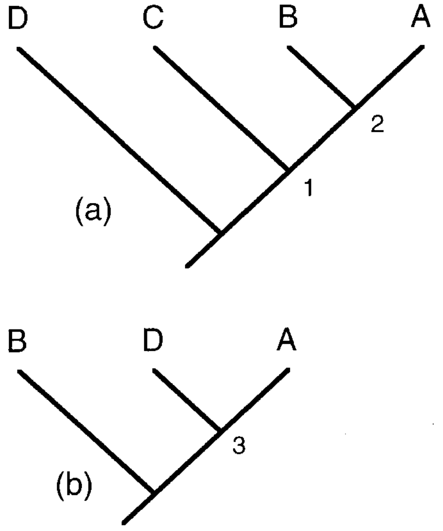


(c)

	Components		
Taxon	1	2	3
A	1	1	1
B	1	1	0
C	1	0	?
D	0	0	1

FIGURE 1. Purvis's (1995b) conflicting source trees (a, b) (with components numbered), and the combined element matrix (c). MRP analysis of the matrix results in tree a. Purvis's method results in an unresolved CCT.

unmodified MRP (Ragan, 1992b), parsimony analysis of the elements derived from one source tree recovers the correct topology (Purvis, 1995b).

Ronquist (1996) demonstrated that this modification to the coding procedure is flawed. He showed that the information content of matrices generated with Purvis's (1995b) method is less than that generated by standard additive binary coding and demonstrated that Purvis's method does not always achieve its goals. Also, because of the specific manner by which Purvis's coding adds missing data to the matrix, the relative positional stability of taxa is altered (Ronquist, 1996; his Fig. 3) so that the position of a taxon on the composite tree is influenced more by source trees on which it is further from the base. We would add that although the zeros replaced under Purvis's method are not strictly informative because they denote the lack of membership of taxa in components, they provide essential, restrictive information regarding the position of a taxon on its source tree that might become important when its elements are combined with those from other source trees.

Ronquist (1996) concluded that the bias described by Purvis (1995b) was associated not with redundant information but with the relative sizes of the source trees. Purvis's method proportionately reduces the influence of larger trees because they contribute a proportionately larger number of missing data points to the element matrix. Ronquist argued that the difference in the amount of information contributed by each source tree could be removed by inversely weighting each tree according to its number of internal branches (i.e., nodes). However, Ronquist favored weighting based on the support for nodes as measured by Bremer's decay index (Bremer, 1988) or the bootstrap (Felsenstein, 1985), both of which he implied would also compensate for any size bias.

Ronquist's (1996) analyses focused largely on the ability of various coding and weighting options to represent the information in a single source tree (and the original data set), rather than the ability of MRP to appropriately combine the information provided by multiple source trees in a single topology. Our discussion focuses more on the latter.

PROPERTIES OF MRP

Matrix Elements versus Characters

We have referred to the coded components of source trees as "matrix elements" rather than as "characters" because the two are not equivalent (Baum and Ragan, 1993). Characters are attributes of organisms. In contrast, a matrix element refers to a component of a tree and is a membership criterion. Matrix elements also differ from characters in that groups of elements representing a single source tree are necessarily congruent, forming a clique of elements. Conflicts between matrix elements from different source trees often involve other elements from their respective source trees, with members of each clique of elements supporting one another.

Although characters are also occasionally derived by using additive binary coding, the requisite use of additive binary coding in MRP results in nonindependence among matrix elements. This nonindependence implies that, compared to standard character matrices, goodness-of-fit indices should be interpreted differently (e.g., the CI would have a higher minimum value and would presumably measure the agreement among source trees) and some statistical methods may be inappropriate (e.g., bootstrap analysis; see Felsenstein, 1985; Purvis, 1995b).

Does MRP Combine Nodes or Trees?

Although MRP is described as a method for combining trees (Baum, 1992; Ragan, 1992b; Purvis, 1995b; Ronquist, 1996), matrix elements represent the nodes on those source trees. As a result, source trees can contribute different amounts of information; trees with more nodes (due to having more taxa or greater resolution or both) contribute more elements to the matrix and therefore generally have a greater influence on the topology of the composite tree. Thus, the claim that MRP eliminates the effect of data matrix size (Baum, 1992; Ragan, 1992b) applies to the number of characters but not to the number of taxa.

However, the claim that MRP favors larger source trees (Ronquist, 1996) is inaccurate. Despite the difference in size of the two source trees in Figure 2, clade (A, B, C) is unresolved in the CCT (Fig. 2c) because each source tree provides one (conflicting) piece of information regarding its resolution. The relative number of matrix elements provided by the source trees determines the resolution of regions of conflict ([A, B, C] in this example). The placement of taxa D–H is determined by the larger tree, which provides the only information concerning their positions. In other words, a size bias occurs only when the "missing nodes" (missing taxa or polytomies) are located within the region of conflict among the source trees. In Purvis's (1995b) example (Fig. 1), the region of conflict coincides with the entire tree.

This bias towards trees with more information (nodes) in regions of conflict may or may not be perceived as a problem. Trees with more nodes possess more hierarchical clustering information; this provides the basis for the argument that these trees should have a greater contribution to that region of the composite tree. In Figure 1, MRP results in the topology of the larger tree because both elements from Figure 1a support (A, B)D and therefore over-

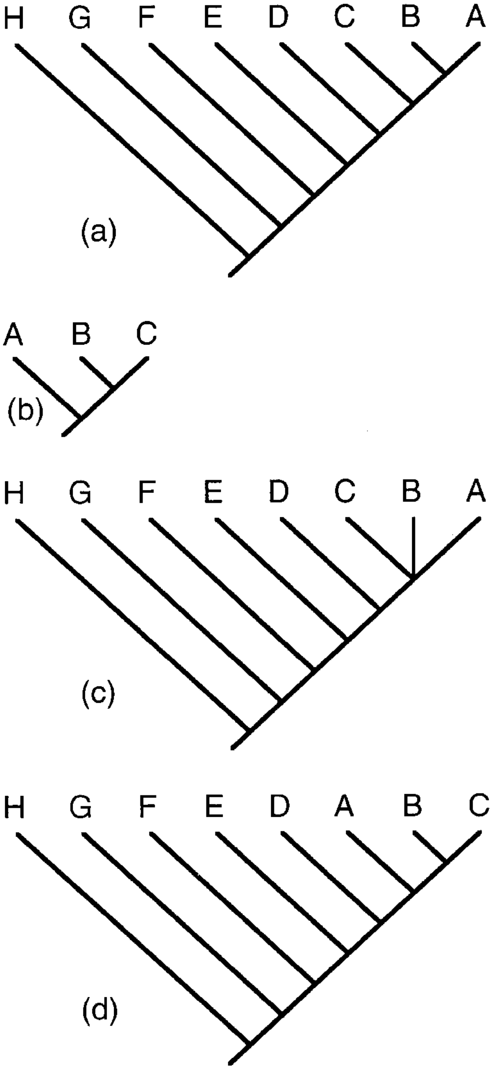


FIGURE 2. Demonstration of the localized nature of the size bias in MRP. Although tree a is much larger than tree b, the CCT (c) is unresolved in the region they share (A, B, C), reflecting the equal information content of the two trees in this region. (d) The intuitively erroneous result that results from inversely weighting the source trees according to their number of nodes.

rule the single conflicting element from Figure 1b. From this node-based perspective, whereby trees are viewed as solely the sum of their nodes, any size bias associated with MRP is appropriate.

From a tree-based perspective, however, each source tree is seen as a holistic entity that should have equal input into the topology of the composite tree. Purvis (1995b) noted that no placement of C on Figure 1b yields agreement with Figure 1a; as a result, he argued that the composite tree should be unresolved and that the bias of MRP toward the larger tree was inappropriate. Purvis's (1995b) argument, and this perspective as a whole, tacitly assumes that the addition of C to Figure 1b will not alter other relationships on that tree (see also Arnold, 1981; Donoghue et al., 1989; Lecointre et al., 1993), possibly to a pattern more similar to that on Figure 1a.

The use of MRP under a tree-based perspective requires correction for the bias toward trees with more nodes in regions of conflict. Inversely weighting elements based on the number of nodes on the source tree so that the total weight of each tree is equal (Ronquist, 1996) fails when the region of conflict forms only part of one or more of the source trees; it ignores the local nature of the size bias. For example, if the nodes on the trees in Figure 2 are inversely weighted, the composite tree includes A(B, C) (Fig. 2d); in contrast, unweighted MRP leaves (A, B, C) unresolved on the CCT, the intuitively correct result. Thus, weighting must be applied only to the conflicting regions between source trees, which becomes increasingly complex as more source trees are combined.

Differentiation between node- and tree-based perspectives is relevant methodologically only when the source trees have different terminal taxa or distributions of resolved nodes. Until recently, techniques that summarized multiple trees on a single topology dealt with multiple equally most-parsimonious trees (MPTs) derived from a single data set, among which differences in the number of nodes arose only from differences in resolution. With the development of MRP and other methods that combine trees with different terminal taxa, the question of whether a tree is equal solely to the sum of its nodes (see Adams [1986] for a discussion of this issue within a different context) has become an issue.

Novel Components

In the discussion of his composite tree synthesizing previous phylogenetic hypotheses concerning extant primates, Purvis (1995a: 414) claimed that "because all of the information on which it is based has been published previously, the composite tree cannot contain any clades that have not been implied by any previous study." Although this statement was intended to apply only to his modified coding method (A. Purvis, pers. comm.), it is also true of most consensus methods, which simply accept or reject components on the basis of agreement among the source trees. One exception is Adams consensus (Adams, 1972), which resolves disagreement among source trees by placing taxa of uncertain position as part of a polytomy at the least inclusive common node (Wilkinson, 1994). In contrast, the use by MRP of parsimony to produce the composite tree provides the potential that incongruence among the matrix elements may generate novel clades. This potential may be increased by the ability of MRP to combine trees with different terminal taxa.

In Figure 3, the CCT (Fig. 3c) includes a clade (marked with a solid circle) that is not present in either source tree (Figs. 3a, 3b). The CCT resembles Figure 3a except that *Pteronura* clusters with *Lutrogale*, as on Figure 3b. *Pteronura*'s membership in three components on Figure 3b appears to outweigh the evidence for a more basal position (Fig. 3a). The overall resemblance of the CCT to Figure 3a reflects the polytomies (lower information content) in Figure 3b.

The creation of novel clades appears to be uncommon. In the results of Bininda-Emonds et al. (in review), only 8 of the 198 nodes (4.0%) on the 13 composite trees occurred on none of the 274 source trees. The apparent rarity of novel clades may be related to the congruence among the matrix elements derived from each source tree, which may reduce the ability of individual elements from different source trees to interact in new combinations to form novel components. Most novel clades found in our analyses occur on only a fraction of a set of

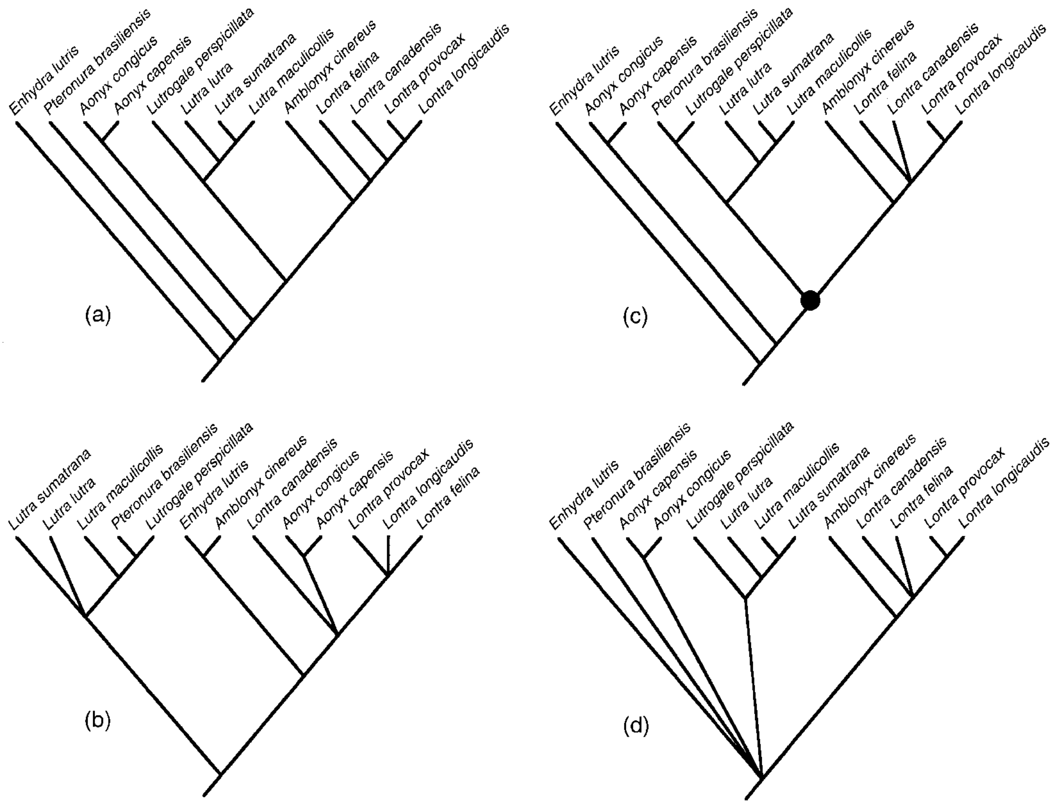


FIGURE 3. Creation of novel components using MRP (lutrine data from van Zyll de Jong, 1987). (a, b) Two source trees. (c) CCT with a component (●) that is not found in either tree a or tree b. (d) CCT generated when reversals are prohibited. The topology is similar to that of an Adams consensus tree.

MPCTs and therefore are subsumed within a polytomy when the MPCTs are summarized by use of a strict CCT.

Is MRP a Consensus Technique?

Although both conventional consensus techniques and MRP combine source trees based on their nodes, there are fundamental differences between them. Most consensus techniques look for the common occurrence of (agreement among) constituent nodes among source trees; conflict usually results in a polytomy (exceptions: majority rule and other consensus trees of the M_l family [McMorris and Neumann, 1983], which retain components found on a certain percentage of the trees). Within source trees, nodes are treated in isolation; individual components are either accepted or rejected (based on information from other source trees), and support for less-inclusive nodes by more-inclusive ones consists only of allowing those nodes with which they are congruent to occur on the consensus tree. Thus, although standard consensus techniques look for agreement among components, they are tree-based, in that source trees are combined equally, regardless of their size.

In contrast, in MRP, elements representing more-inclusive nodes directly support those of less-inclusive ones. For example, in Figure 1a the grouping of A and B to the exclusion of D is supported by both nodes on the tree: (A, B, C)D and (A, B)C, D. When that tree is combined with the smaller tree, (A, D)B, the composite tree includes (A, B). With standard consensus techniques, the contradiction of (A, B) by the second tree results in A and B forming part of a polytomy. The latter also occurs when using Lanyon's (1993) modified semistrict consensus algorithm, which can handle trees with different terminal taxa. This feature of MRP results from it being node-based and arises through the use of additive binary coding to produce the element matrix and the use of parsimony to resolve the incongruence among elements from different source trees.

MRP has often been considered a consensus technique for combining the information in multiple data sets (e.g., DeSalle, 1994; Williams, 1994; Bruneau et al., 1995; de Queiroz et al., 1995), particularly because it eliminates the effect of differences in character number. Although both MRP and consensus techniques appear superficially to combine trees, clustering them on this basis conceals their different mechanics. Also, the ability of MRP to incorporate information about signal strength in the source matrix (see below) sets it still further apart from consensus techniques. Given the fundamental differences in how MRP combines source trees, we argue that MRP is not a consensus technique.

OTHER POSSIBLE MODIFICATIONS TO MRP

Prohibiting Reversals

The use of parsimony algorithms that allow reversals entails that clades in the composite tree can be supported in whole or in part by 0s in the element matrix. In the results of Bininda-Emonds et al. (in review), between 39 (19.7%) and 81 (40.9%) of the 198 nodes (DELTRAN vs. ACCTRAN optimization, respectively) were supported by one or more 0s. A few nodes were supported by more 0s than 1s, particularly under ACCTRAN optimization (Fig. 4).

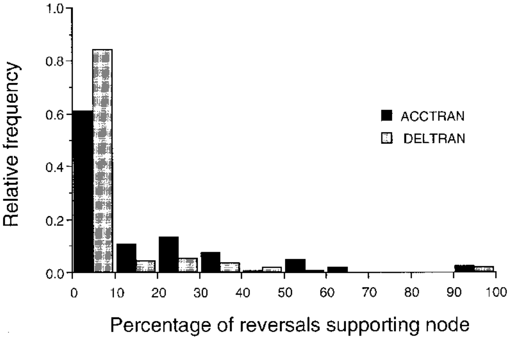


FIGURE 4. Frequency histogram showing the percentage of reversals supporting each of the 198 nodes of Bininda-Emonds et al. (in review) under both ACCTRAN and DELTRAN optimizations. Most nodes were not supported by any 0s.

Clustering on the basis of 0s seems inappropriate in MRP because support for a clade is based in part on taxa that share a lack of membership in the components on the source trees. Unlike conventional character data, in which transformation in either direction between character states can be considered potential evidence for clustering taxa, in MRP only the 1s in the element matrix represent membership in components and therefore seem appropriate for grouping taxa. This suggests that the parsimony algorithm used in MRP should not allow reversals.

To test the effect of prohibiting reversals, we reanalyzed 19 recent "total evidence" studies (sensu Kluge, 1989; Table 1), using MRP to combine the topologies of the process partitions. Analyses were conducted with and without reversals, and differences in topology between the (consensus) composite trees and the total evidence tree were quantified by using the symmetric difference metric (Penny and Hendy, 1985). Despite the variation among the 19 studies in partition size, number of taxa, and disagreement among the partition trees, the effect of prohibiting reversals was usually minor. In eight cases, MRP with and without reversals produced the same CCT; in five cases, prohibiting reversals yielded a CCT that was more similar to the total evidence tree; and in six cases, allowing reversals produced a CCT that was closer to the total evidence tree. The topologies with and without reversals were markedly different from each other in only three instances, and in only two of these (Bininda-Emonds and Russell, 1996; Bremer, 1996) did the source trees conflict strongly.

The example in Figure 5 may suggest why prohibiting reversals does not necessarily produce the better result. Although allowing reversals produces the intuitively correct result in this example, the reversal (Fig. 5c) involves only taxon B (i.e., it does not support a clade) and simply represents the incongruence of the position of B on the CCT with that on one of the source trees (Fig. 5a). This example suggests that MRP might perform better if it were based on an algorithm that prohibited reversals on internal branches but allowed them on terminal ones.

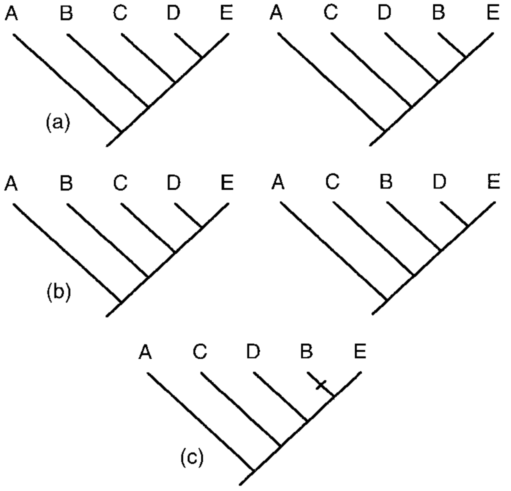


FIGURE 5. Comparison of standard MRP and MRP without reversals. (a) Source trees. (b) Two equally parsimonious composite trees generated by MRP without reversals. (c) Additional tree produced with reversals (location marked with a bar). The three MPCTs based on standard MRP seem to better cover the range of possible positions of taxon B on the source trees.

The question of whether to allow reversals in MRP analyses requires further study. Our sample shows that prohibiting reversals usually produces only minor differences in topology. Prohibiting reversals also does not markedly alter the number of novel clades (which may be supported largely by 0s); reanalysis of the source trees in Bininda-Emonds et al. (unpubl.) with reversals prohibited increased the number of novel clades from 8 to 10. These reanalyses also suggest that MRP without reversals is somewhat conservative, frequently producing a CCT that, like Adams consensus trees, places incongruent components (e.g., Fig. 3d) or particular members of those components (e.g., taxon B in Fig. 5) in basal positions.

Increasing the Informativeness of Source Tree Polytomies

The number of nodes on a source tree, and consequently the number of matrix elements associated with the tree, is reduced by polytomies. Thus, for a given number of terminal taxa, trees with more polytomies have relatively less influence on the pattern of the composite tree in regions of conflict than do completely dichotomous trees. The use of additive binary coding in MRP makes this method unable to distinguish between polytomies that are considered "hard" (representing putative multiple speciation events) and those that are considered "soft" (representing either a lack of resolution or conflicting resolutions) (Maddison, 1989); all polytomies are considered unresolved. While this is appropriate for soft polytomies that do represent a lack of resolution, it is inappropriate for polytomies that are purported to be hard (and therefore fully resolved), and for soft polytomies that represent conflicting solutions, such as those on a strict consensus tree.

We have no suggestions for counteracting any perceived bias this causes against hard polytomies. Nonetheless, the problems in identifying hard polytomies makes this largely a nonissue. For soft polytomies that represent conflicting resolutions, the goal is to retrieve those resolutions of the polytomy that occur among the MPTs. Although a case can be made for using the consensus solution on practical grounds when there are large numbers of MPTs (Ragan, 1992b), ideally, the more-resolved topologies of the MPTs and not that of the less-resolved consensus should contribute to the element matrix.

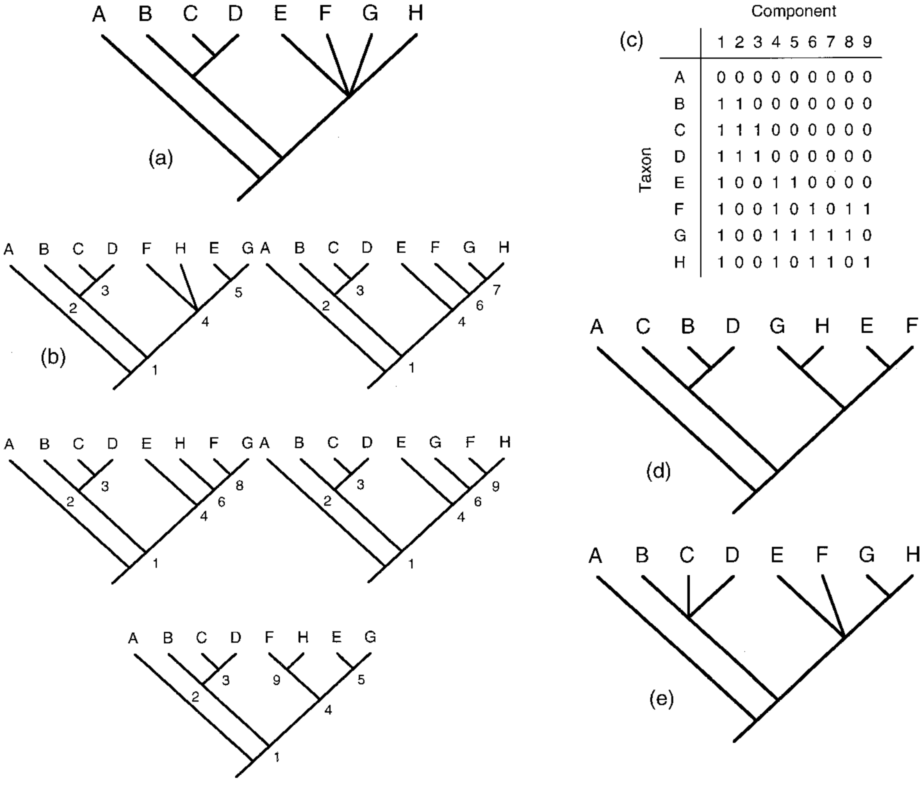
This can be accomplished by coding each unique component on any one or more trees in a set of MPTs as an element in the combined matrix (see Fig. 6). These elements can be handled in at least two ways. Weighting each component according to its frequency among the MPTs is the equivalent of Ragan's (1992b) suggestion of individually coding and including each MPT in the element matrix. In this procedure, the influence of a clade on the pattern of the composite tree depends on its frequency among the MPTs: clades that occur on more of the MPTs will have a greater influence, and any clade occurring on only some MPTs will have less weight in the analysis than will clades supported by data sets producing only one MPT. Alternatively, one of us (H.N.B.) argues that the above weighting is inappropriate. Because each of the shortest trees obtained from a single data set is equally parsimonious, overall evidence in the data set for each clade on any one or more of the MPTs is equal and so they should all receive equal weight.

In either instance, weighting of these elements relative to those based on other source trees is not necessary. Although the number of elements derived from data sets that produce more than one MPT will usually be larger than that associated with a single MPT with the same number of taxa, either the frequency-dependent weighting of, or the incongruence among, elements representing alternative resolutions of polytomies on consensus trees negates the increased influence their increased number might have on the topology of the composite tree (see Fig. 6).

Weighting Elements Based on Evidential Support

Because MRP generates composite trees based solely on the topologies of the source trees, there is no inherent consideration of either the overall support for the topology of a source tree or for the differential support for the nodes on that tree (Rodrigo, 1993; Galtier and Gouy, 1994; Bandelt, 1995; Bruneau et al., 1995). Although bypassing the original data is necessary in some instances, it has been argued that the differential support for the overall topologies of, or different nodes on, the source trees could or should be used in deriving the composite tree whenever possible (Purvis, 1995b; Ronquist, 1996).

Potential measures of support for entire source trees include goodness-of-fit indices (Farris, 1989; Baum, 1992), PTP values (Faith and Cranston, 1991), or total support (Källersjö et al., 1992). Potential means of weighting based on differential support for individual clades on source trees include bootstrap frequencies (Felsenstein, 1985), Bremer support (Bremer, 1988), the number of unique synapomorphies (Kluge, 1989), or T-PTP probabilities



Taxon	1	2	3	4	5	6	7	8	9
A	0	0	0	0	0	0	0	0	0
B	1	1	0	0	0	0	0	0	0
C	1	1	1	0	0	0	0	0	0
D	1	1	1	0	0	0	0	0	0
E	1	0	0	1	1	0	0	0	0
F	1	0	0	1	0	1	0	1	1
G	1	0	0	1	1	1	1	1	0
H	1	0	0	1	0	1	1	0	1

FIGURE 6. One method of coding source trees with polytomies. (a) Consensus tree. (b) Five MPTs (the nine unique components are numbered). (c) Matrix consisting of one element for each of the numbered unique components. (d) Conflicting source tree. (e) CCT resulting from unweighted MRP analysis of the matrix c and the elements derived from the conflicting source tree d.

(Faith, 1991). Ronquist (1996) showed that weighting elements from single source trees based on either Bremer support or bootstrap values improves the correlation between tree lengths obtained from the element matrix and those obtained from the original character data. Weighting by Bremer support also causes the decay values to be reproduced exactly (Ronquist, 1996). Thus, these methods apparently solve a major criticism of MRP, namely, that it fails to incorporate relative support for nodes into the analysis.

The use of any of these measures of support requires that two conditions be met. First, the chosen metric must be available for all source trees. Because source trees lacking the metric should not be ignored, this requirement may in some instances preclude the use of weighting based on evidential support. The use of multiple metrics might be feasible in some of these cases; however, the necessity that they all yield equivalent, standardized information will probably prevent this. Second, the values of the chosen metric must provide a comparable measure of the relative support for a given node across studies, regardless of the characteristics of the original data and the algorithm that produced the source tree. Bremer support, total support, and the number of unique synapomorphies are influenced by the number of characters in the original data matrices and need to be standardized across data sets. Bremer support cannot be used when components on multiple MPTs, rather than those on their consensus, are coded because the Bremer support values for components that do not occur on all MPTs are zero and so their associated elements would have a weight of zero. The bootstrap may be less influenced by the differential characteristics of data sets (i.e., values are probably more standardized), but this issue requires further study.

Because all these weighting schemes based on support for entire trees or individual nodes operate on the elements in the matrix, they do not offset the inherent size bias of MRP (contra Ronquist, 1996). The problems associated with weighting the element matrix to make MRP tree-based are only compounded if weighting based on evidential support in the original data is also desired.

CLOSING STATEMENTS

MRP is unique in that it combines source trees by using additive binary coding to convert the hierarchical information within them into an element matrix and using parsimony to derive the composite tree; these mechanics clearly differentiate MRP from standard consensus techniques, despite being associated with them by many authors. MRP is inherently node-based. The influence of individual source trees on the composite tree depends on their size and resolution, and the matrix elements derived from a single source tree directly support one another. As a result, source trees are not combined equally. In contrast, consensus techniques are tree-based. Although they also operate at the node level, components are treated in isolation and are simply accepted or rejected based on the agreement among the source trees. Therefore, all trees have an equal vote regarding the topology of the consensus tree. This difference is fundamental, and is the basis for our conclusion that MRP is not a consensus technique. The difference in both the mechanics and results of MRP, as compared to those of consensus techniques, may require a shift in current thinking as to appropriate methods for combining source trees. At the very least, MRP is providing a synthesis different from consensus techniques of the information in a set of source trees.

MRP has been promoted as a "total evidence approach" (Purvis, 1995b:253) for data sets that are not amenable to standard character congruence methods (e.g., Kluge, 1989). The data in Table 1 suggest that MRP often falls short of this goal. In only 3 of 19 cases does the topology produced by MRP match the total evidence tree, and in several instances the differences between the results of the two methods are marked. MRP tends to collapse clades found on the total evidence tree, producing more polytomies, but taxa are also occasionally placed in different positions. There is no obvious relationship between the number of partitions and the ability of MRP to match the total evidence tree.

The use of parsimony allows for weighting of the matrix elements to adjust for inherent biases in the method or to incorporate additional information. To date, attempts to adjust

TABLE 1. Comparison of MRP with and without reversals in 19 total evidence studies. The CCTs obtained from the respective MRP analyses of the partitions were compared with the total evidence topology and each other using Penny and Hendy's (1985) symmetric difference metric.

Study	No. taxa	No. partitions	With reversals vs. total evidence	Without reversals vs. total evidence	With vs. without reversals
Kluge, 1989	11	2	3	3	0
Vane-Wright et al., 1992	10	2	1	3	2
Cundall et al., 1993	18	3	13	13	0
Eernisse and Kluge, 1993	5	7	1	0	1
Wheeler et al., 1993	26	3	15	17	12
Kim and Jansen, 1994	7	4	2	0	2
Lundrigan and Tucker, 1994	12	3	0	0	0
Omland, 1994	9	2	1	1	0
Vrana et al., 1994	31	2	9	7	4
Yoder, 1994	13	2	7	5	2
Littlewood and Smith, 1995	45	3	9	10	1
Paterson et al., 1995	18	3	6	7	1
Tehler, 1995	5	2	2	1	1
Zhang, 1995	8	2	0	0	0
Bininda-Emonds and Russell, 1996	27	7	22	32	20
Bremer, 1996	33	2	12	16	8
Friesen et al., 1996	25	2	14	14	0
Sites et al., 1996 (*Enyalioides* outgroup)	14	3	4	4	0
Sites et al., 1996 (*Oplurus* outgroup)	14	3	0	0	0

for any perceived bias toward more-informative (i.e., larger, more resolved, or both) regions of source trees (e.g., Purvis, 1995b; Ronquist, 1996) to make the method tree-based have been unsuccessful. The appropriateness of correcting for this bias is arguable; however, without this correction, MRP should not be used if a tree-based result is desired. With certain limitations, weighting provides a means of incorporating the differential support for entire trees or individual clades present in the original data into the analysis, while still allowing the composite tree to be based primarily on the hierarchical information in the source trees. These modifications might allow MRP to more closely approximate a "total evidence" result.

Baum (1992) noted that detailed study of the properties of MRP, empirical testing of its results, and comparisons with standard consensus techniques had not yet been conducted. Subsequent analyses (Baum and Ragan, 1993; Rodrigo, 1993; Purvis, 1995b; Ronquist, 1996; this study) have considered some of these issues. Issues requiring further study include the appropriateness of allowing reversals within matrix elements (on either all or only terminal branches) and the ability of MRP to replace total evidence analyses when the data are not suitable for the latter. These studies are essential to assess the potential contribution of MRP and its variants to phylogenetic inference.

ACKNOWLEDGMENTS

The first author thanks Andy Purvis for introducing him to MRP and for many fruitful initial discussions regarding the technique, and acknowledges Alberta Heritage, the United Kingdom's Overseas Research Scholarship plan, and a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship for funding the project. Andy Purvis also pointed out the counterexample used in Figure 2. Fredrik Ronquist kindly supplied us with a preprint copy of his manuscript. David Cannatella, Paul Harvey, Andy Purvis, Alan Rodrigo, and Fredrik Ronquist made constructive comments on an earlier version of this paper.

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Received 22 July 1996; accepted 10 September 1997
Associate Editor: D. Cannatella

Syst. Biol. 47(3): 508–519, 1998

Why Morphometrics Is Not Special: Coding Quantitative Data for Phylogenetic Analysis

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Systematists often use qualitative descriptions of shape in phylogenetic analyses, but several biologists object to phylogenetic analyses using quantitative descriptions of those same shapes (Pimentel and Riggins, 1987; Felsenstein, 1988; Mickevich and Weller, 1990; Garland and Adolph, 1994). In a previous paper (Zelditch et al., 1995), we argued that the problem with phylogenetic analysis of quantitative shape data lies in the particular methods traditionally used to quantify shapes, not in quantification per se. In addition, we demonstrated that some of the more serious objections to using morphometric data in phylogenetic analyses are removed by using landmark-based morphometric methods developed by Bookstein (1991). Although we demonstrated that phylogenetic analysis of quantified shape variables is valid in theory, some practical problems remain. In this paper, we address the major remaining problem, that of coding: specifically, the problem of recognizing divergent character states.

Even a brief survey of the literature shows that coding is a complicated task in which several obstacles must be overcome (see Mickevich and Weller, 1990; Mabee and Humphries, 1993; Wilkinson, 1995). In this paper, we focus on one particular obstacle: evaluation of the diversity of a feature to determine which sets of taxa are similar in that feature. These judgements of similarity (and differences) are the foundations on which inferences of homology and monophyly are based. If these judgements employ inappropriate criteria, then those inferences are apt to be misled, and the resulting phylogeny is likely to be wrong.

Several biologists have argued that there can be no valid criteria for dividing quantitative data into discrete states because quantitative traits are inherently continuous (Pimentel and Riggins, 1987; Felsenstein, 1988; Garland and Adolph, 1994). In fact, they claim that coding quantitative data introduces artificial distinctions even if the observed distribution is discontinuous. This claim has even been parlayed