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Properties of Supertree Methods in the Consensus Setting

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"Supertrees are in essence not more than generalised consensus trees. Perhaps it would be judicious to reach a satisfactory consensus on the use of consensus trees before tackling their generalisation." Bryant (2003:164).

Supertree methods (SMs) are techniques for inferring (super)trees from sets of (input) trees. Classical consensus methods are SMs that were designed for the special case where input trees have identical leaf sets. The need for methods that can also combine information from input trees with nonidentical leaf sets has led to many alternative SMs. Some of these SMs are generalizations from conservative consensus methods (strict and semistrict) that do not resolve input tree conflicts (e.g., Gordon, 1986; Goloboff and Pol, 2002). Our focus here is on more liberal SMs, those capable of resolving conflicts among input trees. Liberal SMs comprise the majority of described methods and have been the most used in practice by biologists seeking well-resolved phylogenies. However, today's practitioners are confronted with choosing among a potentially bewildering array of liberal SM(s).

Wilkinson et al. (2004) argued that nonarbitrary, rational choice among liberal SMs would best be guided by knowledge of the comparative accuracy of alternative methods. However, there have been few comparisons of accuracy using simulations (Bininda-Emonds and Sanderson, 2001; Chen et al., 2003; Eulenstein et al., 2004; Lapointe and Levasseur, 2004; Ross and Rodrigo, 2004) over a restricted range of conditions. Thus, Wilkinson et al. (2004) also discussed a number of properties that they suggested provide surrogates for accuracy and might therefore be expected of any SM. One of these, that input tree conflicts should be resolved independently of input tree shape, was investigated by Wilkinson et al. (2005a), who used a simple example (Fig. 1) and simulations to demonstrate input tree shape effects with 8 of the 14 methods they investigated, including the widely used matrix representation with parsimony (MRP) of Baum (1992) and Ragan (1992). Here we introduce a class of sub-Pareto properties that we argue constitute particularly weak expectations of how accurate SMs should handle consensus problems. We then use the same example to substantiate and extend results reported in Wilkinson et al. (2004) and to demonstrate that seven of the liberal SMs that are sensitive to input tree shape also lack some seemingly reasonable consensus properties. Lastly, we consider the relevance of these properties to choice and

design of SMs. We stress that our focus here is on the consensus setting and that we are not considering the more general supertree case.

PRELIMINARIES

We are concerned with leaf-labeled phylogenetic trees that display exclusively branching (i.e., nonreticulate) relationships among the included terminal taxa (the leaf set of the tree). A split is a tree with one internal branch (i.e., with edge of degree >2) and a quartet is a split on four leaves. For a given leaf set X , a *full* split of X is bipartition Y/Z such that $Y \cap Z = \emptyset$ and $Y \cup Z = X$. A triplet is a rooted split on three leaves equivalent to a quartet where one leaf is the root. Similarly, a component is a rooted full split equivalent to a full split where one leaf is the root. A nesting $Y < Z$ is a statement that leaf set Y has a more recent common ancestor than leaf set $Y \cup Z$ and is defined only for rooted trees. Examples of the types of information displayed by trees are shown in Figure 2. We say that a tree displays all and only the relationships (splits, nestings) that must be true if the tree is true (and thus can be produced by pruning its leaves and/or collapsing its branches) and that a tree T_1 displays a tree T_2 if T_1 displays all the relationships displayed by T_2 . A Pareto split is a split that is displayed by every member of a set of input trees. Relationships are compatible if there exists some single tree that displays them all; otherwise, they are incompatible (conflict). We interpret all polytomies (in supertrees and input trees) as soft; i.e., as compatible with (and displayed by) their possible resolutions, and all definitions pertain to just this case. We focus on rooted trees because some SMs are undefined for unrooted trees. Full descriptions of the SMs considered here are given by Wilkinson et al. (2005a). Some of the SMs we consider may return equally optimal supertrees. In that case, we say a property holds for a method if it holds for all, and that it does not hold if it does not hold for any, of the optimal supertrees. Although other consensus methods have been employed, common practice has been to construct a strict consensus of all equally optimal supertrees, and we also investigate the properties of such consensus SMs in the special case of consensus. For a given SM, the corresponding consensus SM is indicated by an asterisk (e.g., Purvis MRP* is the method returning the strict consensus of the optimal Purvis MRP supertrees).

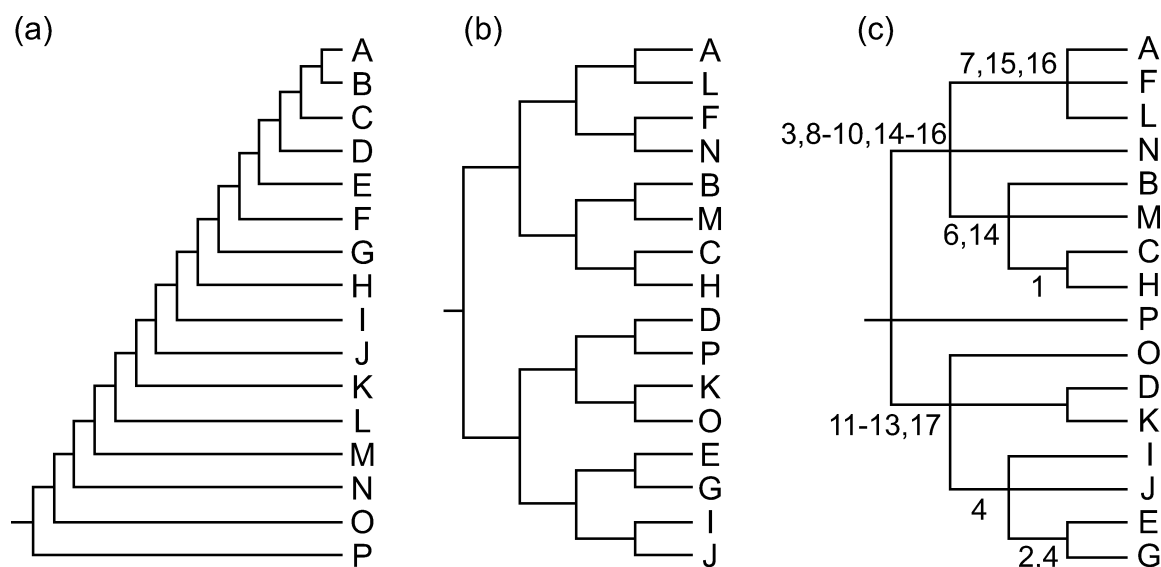


FIGURE 1. Two highly incongruent binary input trees of equal size and information content that are maximally unbalanced (a) or maximally balanced (b). Classical consensus trees for this problem are unresolved except for the Adams consensus (c), which is identical to the MinCut and modified MinCut supertrees in this case. Numbers indicate branches that display relationships in the strict reduced consensus trees (Table 1).

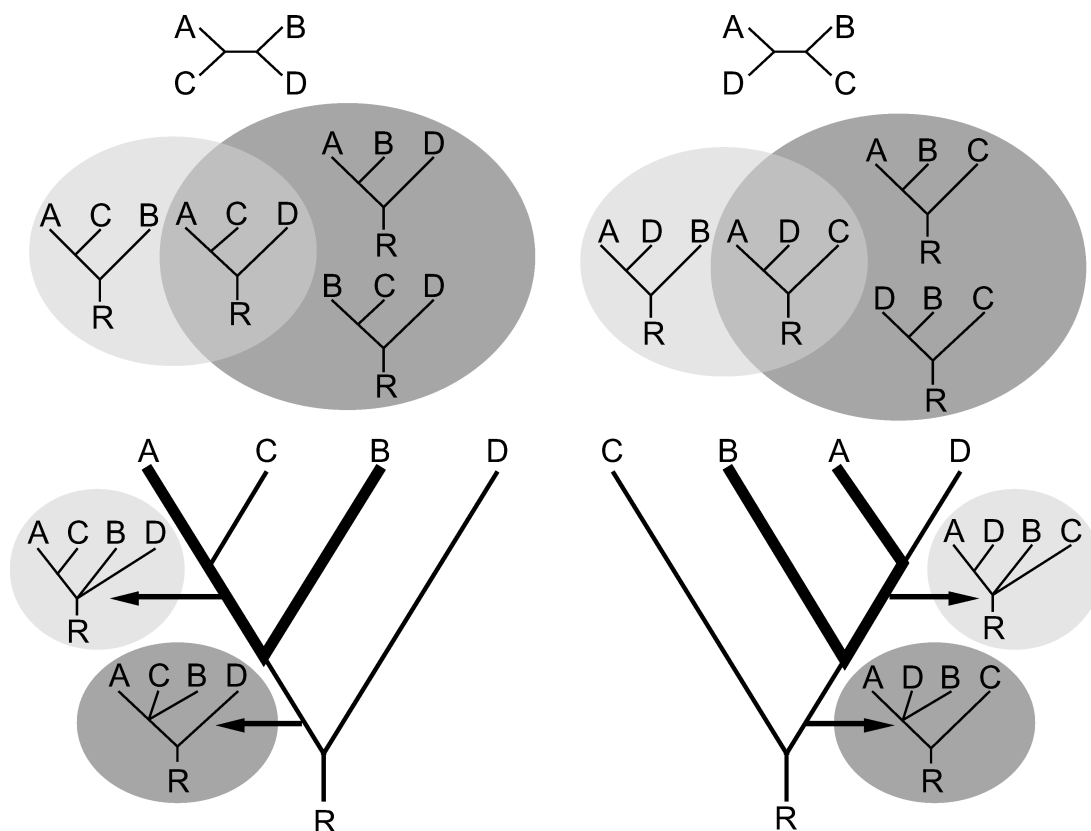


FIGURE 2. Two rooted trees and examples of the relationships they display. Each tree displays two components (relationships displayed by an internal branch indicated by arrows). Each tree also displays four triplets indicated as quartets where one of the leaves is the root (R) and one additional quartet that does not include the root. Each component entails a set of triplets (indicated by corresponding shading). None of the components or triplets are displayed by both trees, but they display one common nesting ($AB < CD$) shown by the thickened line, indicating that the ancestor of A and B is more recent than the ancestor of A, B, C, and D.

SOME CONSENSUS PROPERTIES

We focus here on how SMs handle consensus problems, asking whether they have consensus properties that seem desirable. There are good reasons for focusing on consensus problems. What might be reasonably expected of their solutions is currently a little better understood for consensus than for supertree problems more generally, making consensus a relatively tractable special case. Further, if an SM can be shown not to satisfy an expectation in the consensus case, then it cannot satisfy any supertree property that is a generalization from the consensus property. Lastly, SMs are sometimes used as consensus methods (e.g., Cardillo et al., 2004).

Pareto relationships, e.g., particular components, triplets, or nestings that are displayed by every input tree, are interesting because they are maximally supported and uncontradicted by the input trees. Inasmuch as support is correlated with accuracy, we might reasonably expect liberal SMs to return supertrees that include any Pareto relationships in the special case of consensus. Methods with this property are said to be Pareto on that kind of relationship (i.e., on components or triplets or nestings). In consensus problems, a relationship is supported if it is displayed by one or more input trees (Bininda-Emonds, 2003; Wilkinson et al., 2005b). Other relationships are unsupported. Inasmuch as unsupported relationships are less likely to be accurate than supported ones, we might reasonably expect liberal SMs to return supertrees that do not include unsupported relationships when handling consensus problems. Methods with this property are said to be co-Pareto on that kind of relationship (see also Huson et al., 2004, for a generalization beyond consensus).

Possible Pareto and co-Pareto properties of consensus methods (with respect to components, triplets, or nestings) have been discussed as consensus axioms (e.g., Adams, 1986; Bryant, 2003; Day and McMorris, 2003a). Although this terminology may suggest their desirability is self-evident, we see these particular properties as more or less compelling requirements of acceptable methods because of their relation to support and thus to expected accuracy. Pareto axioms require that the best supported relationships are in the consensus, and co-Pareto axioms ensure that the consensus does not include unsupported relationships that "come out of nowhere" (Day and McMorris, 2003b:54).

Pareto and co-Pareto properties are logically independent (a method that is not Pareto on, for example, triplets may be co-Pareto on triplets and vice versa) but both entail the weaker expectation, *that no relationship displayed by the consensus conflicts with any Pareto relationship*. We call methods with these consensus properties, which have not been previously discussed, *sub-Pareto* on, for example, components or triplets or nestings. Relationships conflict when it is not possible for them all to be true, and in the consensus case all conflict is displayed (whereas it may be implied and not directly displayed in supertree problems more generally). A sub-Pareto property pro-

hibits a subset of the unsupported relationships prohibited by the corresponding co-Pareto property: those that conflict with the best supported (i.e., the Pareto) relationships and thus seem least likely to be accurate. Similarly, it prohibits a subset of the ways in which methods might fail to be Pareto, allowing failures of omission (Pareto relationships may be unresolved in the consensus) while prohibiting failures of commission (relationships contradicting Pareto relationship may not be in the consensus). Thus, methods that are Pareto or co-Pareto must also be sub-Pareto but not vice versa.

Equivalently, methods that are not sub-Pareto cannot be either Pareto or co-Pareto. Sub-Pareto properties are very weak and therefore very reasonable expectations of how methods should handle consensus problems. They are intended to prevent the more worrying subset of failures to be Pareto and co-Pareto so as to ensure that particularly objectionable relationships (those that conflict with relationships that are supported by every input tree and are therefore least likely to be accurate) do not somehow appear in the consensus.

Some Pareto, co-Pareto, and sub-Pareto properties on components, triplets, and nestings entail other consensus properties (e.g., Bryant, 1997). These logical relations are summarized in Figure 3. Our main result (see below) is to demonstrate that some methods are not sub-Pareto on triplets. This entails that these methods are neither Pareto nor co-Pareto on triplets, that they are not Pareto, sub-Pareto, or co-Pareto on nestings, and that they are not co-Pareto on components.

RESULTS

The two input trees in our example (Fig. 1a, b) share no components, but there are some Pareto nestings and triplets. Their Adams consensus displays all of these together with some triplets that occur in one of the input trees but are not Pareto (Fig. 1c). The strict reduced consensus (SRC) method (Wilkinson, 1994; Wilkinson and Thorley, 2003), as implemented in RadCon (Thorley and Page, 2000), was used to identify all triplets resolved identically in the two input trees. PAUP* (Swofford, 1998) was then used to filter sets of supertrees to determine whether they conflicted with backbone constraints corresponding to SRC trees. The SRC profile includes 17 trees (Table 1) that jointly display all and only the Pareto triplets of the input trees. Any supertree that conflicts with an SRC tree must conflict with a Pareto triplet, and the method that produced it cannot be sub-Pareto on triplets.

Applied to our example, standard, irreversible, and Purvis MRP, MinFlip, the average consensus, average dendrogram, and duplication-and-loss GTP return supertrees, all of which conflict with one or more of the SRC trees (Table 1) and are therefore not sub-Pareto on triplets. Of these methods, all but the average consensus and average dendrogram return equally optimal supertrees in this case. Their strict consensus trees (Wilkinson et al., 2005a: figure 3) demonstrate that all of the corresponding consensus SMs, except for Purvis MRP* (which gives a

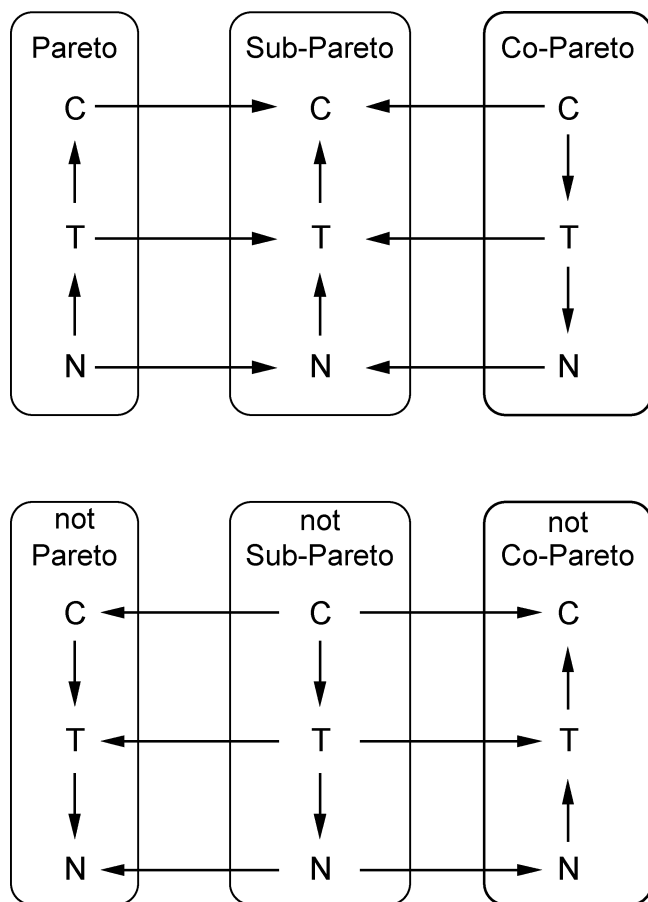


FIGURE 3. Entailment relations among the axioms considered here. C = component; T = triplet; N = nesting. Arrow indicates direction of entailment. The relations follow from the definitions of the axioms and of the relationships. Because of the logical relations between components, triplets, and nestings (components entail triplets entail nestings), if a method is Pareto on nestings, it must include any Pareto triplets and components because these entail Pareto nestings. Conversely, if a method is co-Pareto on components, it must also be co-Pareto on triplets and nestings.

poorly resolved supertree in this case), are also not sub-Pareto on triplets. In the process of supertree construction, relationships (i.e., triplets) that are not present in any of the input trees may somehow be manufactured by these methods at the expense of relationships that are common to the input trees. Standard MRP has been criticized for yielding unsupported clades (e.g., Pisani and Wilkinson, 2002), which, in the consensus case, is to say that this method is not co-Pareto on components. The optimal supertrees and their consensus supertrees confirm that methods that are not sub-Pareto on triplets are not co-Pareto on components—as we know from the logical relations between these axioms (Fig. 3). Most other liberal SMs can be shown or are conjectured to be sub-Pareto on triplets (see Appendix). In contrast, although duplication-only GTP and the MSS methods return supertrees that include all Pareto triplets with our example, we do not know if they are Pareto or sub-Pareto on triplets in general.

Combining previous and our new results (see Appendix) and using the logical relations between the different axioms and the different notions of relationships (Fig. 3), we can summarize what we believe is currently known for each of the 14 SMs (and corresponding consensus SMs) considered here with respect to the consensus properties we have investigated (Table 2). The summary highlights a number of current uncertainties, which may be considered open problems, and some differences among a broad range of SMs in the consensus setting.

DISCUSSION

The increasing number of SMs is confronting workers with methodological choices that force them to seek justifications for any preferences and force us to question common practice. We consider such questioning particularly useful in an emerging discipline. However, there has been relatively little comparison of the extent to which alternative SMs have or lack desirable properties and little discussion of what particular properties are desirable (but see Steel et al., 2000; Goloboff and Pol, 2002; Cotton and Page, 2004; Wilkinson et al., 2004). We have focused here on how liberal SMs handle consensus problems because this is the special case of the supertree problem that is best understood in terms of what might reasonably be expected of their solution. Multiple generalizations from the consensus properties we have discussed might be possible but do not concern us here. Our demonstrations that some methods lack a consensus property necessarily hold for any generalization of the particular property beyond consensus, whereas that a method has a desirable consensus property does not prove it also has any possible generalizations of it outside the special case of consensus. Furthermore, generalizations might not share the logical relations that pertain among the corresponding consensus properties (Fig. 3). Thus, we caution against overinterpreting our results. Our simple example demonstrates that many liberal SMs, including those in most common use, do not handle consensus problems as we might reasonably expect. In particular, they can yield supertrees that display relationships that conflict with what is true of every input tree. We find this worrying because, other things being equal, we expect that what is true of every input tree is most likely to be accurate and that which contradicts what is true of every input tree is least likely to be accurate.

Most consensus methods and many SMs have been shown to be Pareto (and thus also sub-Pareto) on components (i.e., if a component is in every input tree it is in the consensus tree), and no methods are known to definitely lack this property (Bryant, 2003; Table 2; see also Appendix). Its ubiquity underscores that it is a very reasonable expectation in the consensus case. Similarly, although very few classical consensus methods are Pareto on triplets (or nestings), we know of none that is not demonstrably sub-Pareto on triplets. Whereas failure to represent Pareto triplets is not a fatal criticism

TABLE 1. Seventeen strict reduced consensus (SRC) trees for the two input trees of Figure 1 and numbers of conflicting supertrees. Many SMs may return equally optimal supertrees and we can therefore distinguish cases where all (highlighted in bold), some, or none of the supertrees conflict with some Pareto relationship. R is the root. MRP = matrix representation with parsimony. GTP = gene tree parsimony. MSS = most similar supertree. (D) = duplication only; (DL) = duplication and loss.

SRC	Standard MRP	Irreversible MRP	Purvis MRP	MinFlip	Average consensus	Average dendrogram	GTP (DL)
(R,D-G,I-L,N-P,(B,C))			60		1		
(R,H-P,(E,G))			80	8	1		4
(R,D,E,G,I-K,O,P,(A-C))					1		
(R,K-P,(I,J,(E,G)))	2	36	80	16	1		10
(I-P,(C,H))					1		
(R,I-L,N-P,(B,C,H))			60		1		
(R,G-K,M,O-P,(A,F))	2				1		10
(R,O,P,(A-C,F,H,L-N))					1		
(R,I-K,O,P,(A-C,F,H))					1		
(R,G,I-K,O,P,(A-C,F))	2				1		8
(R,L-N,(D,E,G,I-K))			80		1		10
(R,H,L-N,(D,E,G))			80	15			10
(R,F,H,L-N,(D,E))		72	80	10			10
(R,O,P,(N,(B,C,H,M)))		36	60	16	1		
(R,O,P,(M,N,(A,L)))		48		24	1		10
(R,O,P,(M,(A,F,L)))		48		16	1		10
(R,P,(K,O))	2	72		31		1	

of a consensus method, returning consensus trees that conflict with Pareto relationships does seem a serious failing.

Given that it is in principle desirable for liberal SMs to be Pareto, co-Pareto and, a fortiori, sub-Pareto on nestings, triplets, and components in the consensus case, the summary of the consensus properties investigated or inferred here (Table 2) might help in choosing among methods. It does, however, present an incomplete summary of only a few of the desirable properties that might be

taken into consideration in choosing SMs. For example, MinCut methods might be preferred because the time required to compute the output tree grows only polynomially with the number of species (Semple and Steel, 2000), the average consensus because it makes use of branch length information (Lapointe and Levasseur, 2004), and gene-tree parsimony methods because they are based on explicit evolutionary models of the relationship between input (gene) trees and an underlying (species) supertree (Cotton and Page, 2004). It is remarkable that almost all SMs that have objective functions based on unusual asymmetric tree-to-supertree distances and are sensitive to input tree shape (Wilkinson et al., 2005a) are also not sub-Pareto on triplets. The only exception, duplication-only GTP, returns trees that are very similar to the symmetric input tree (Fig. 1b) and does not fail to be sub-Pareto on triplets in this case, but we do not know if this must be true in all cases.

Bryant (2003:164) worried that inferring trees from trees using consensus rules is problematic because their invention "has been guided by combinatorial properties rather than phylogenetic inference criteria." Thus, we are interested in consensus axioms only to the extent that they dictate reasonable criteria for phylogenetic inference. Being sub-Pareto on triplets is intended to be a very reasonable expectation of an SM because of its relation to what seem to be the best supported relationships and thus the best phylogenetic inferences. All other things being equal, we would prefer to use methods that are sub-Pareto on triplets a priori, and we would be disappointed if new methods were developed that did not have this property, without this sacrifice being offset by some advantage in other respects.

Our view contrasts with the increasingly common use of standard MRP, a method that is not sub-Pareto on triplets or co-Pareto on components and that is biased with respect to input tree shape (see also Goloboff, 2005, for critique of this approach). Choice of this method may

TABLE 2. Summary of some consensus properties of SMs with respect to components (C), triplets (T), and nestings (N) demonstrated (in bold) or conjectured in the text or the Appendix. MRP = matrix representation with parsimony. GTP = gene tree parsimony. MSS = most similar supertree. (D) = duplication only; (DL) = duplication and loss. y = has the property; n = lacks the property; ? = unknown; n! = lacks the property due to permitting arbitrary resolutions. (*) indicates that the SM and the corresponding strict consensus SM have the same properties.

Method	Pareto			Co-Pareto			Sub-Pareto		
	C	T	N	C	T	N	C	T	N
Standard MRP (*)	y	n	n	n	n	n	y	n	n
Irreversible MRP (*)	y	n	n	n	n	n	y	n	n
Purvis MRP	y	n	n	n	n	n	y	n	n
Purvis MRP*	y	n	n	?	?	?	y	?	?
MinFlip (*)	y	n	n	n	n	n	y	n	n
Split fit	y	n	n	n!	n!	n!	y	y	y
Split fit*	y	n	n	y	y	y	y	y	y
Triplet fit	y	y	n	n	n!	n!	y	y	y
Triplet fit*	y	n	n	n	y	y	y	y	y
Quartet fit	y	y	n	?	?	?	y	y	?
Quartet fit*	y	n	n	?	?	?	y	y	?
Average consensus	?	n	n	n	n	n	?	n	n
Average dendrogram	?	n	n	n	n	n	?	n	n
MSS	y	?	?	?	?	?	y	?	?
MinCut	y	y	y	n	?	?	y	y	y
Modified MinCut	y	y	y	n	?	?	y	y	y
GTP (DL)/*	y	n	n	n	n	n	y	n	n
GTP (D)/*	y	?	?	?	?	?	y	?	?

be due to ease of implementation, but we think the acceptability of this as justification for relying only upon standard MRP is considerably diminished by the increasing availability of implementations of other methods (e.g., Chen et al., 2004; Creevey et al., 2005). It might be argued that properties displayed using extreme examples will be irrelevant in real cases. Thus, more comprehensive comparisons of the accuracy of existing SMs through, for example, simulation studies would be helpful, as would further consideration of what properties are desirable when input trees have nonidentical leaf sets (e.g., Steel et al., 2000; Goloboff and Pol, 2002). However, we see no reason to expect that methods that lack desirable consensus properties will outperform those that have them.

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APPENDIX

Here we consider those consensus properties reported in Table 2 but not demonstrated in the main text. We stress that we are concerned only with the special case of consensus. Thus, we make no claims or conjectures as to the properties of methods with supertree problems more generally.

Pareto on nestings.—MinCut is the only SM proven to be Pareto on nestings (Semple and Steel, 2000). Given that Page's (2002) modification can only increase resolution, it must share this property. Methods that are Pareto on nestings must also be Pareto on triplets because every Pareto triplet entails a Pareto nesting and any tree that displays the entailed Pareto nesting must display the Pareto triplet. Similarly, methods that are Pareto on triplets must also be Pareto on components because every Pareto component entails a set of Pareto triplets and any tree that displays all the entailed Pareto triplets must display the Pareto component. Thus, MinCut methods are Pareto on triplets and on components. Consequently, they are also sub-Pareto on nestings, triplets, and components. In contrast, methods such as MinCut and the Adams consensus that are Pareto on nestings or on triplets in the consensus setting and that return a single tree cannot be co-Pareto on components (Adams, 1986; Wilkinson, 1994).

Pareto on triplets.—The triplet fit between a supertree and an input tree is the number of triplets displayed by both. Triplet fit SM returns supertrees that maximize the sum of the triplet fits across all input trees. It seems intuitively obvious that Pareto triplets (which are those of maximal weight and which are necessarily mutually compatible and compatible with every other triplet displayed by a set of input trees) must be displayed by any supertree that displays the maximum number of input tree triplets (Pisani, 2002). However, there is as yet no proof of this conjecture and it remains an open problem. We also conjecture that quartet fit is similarly Pareto on quartets and, because triplets are a subset of the quartets (those that include the root), that it also Pareto on triplets. By virtue of being Pareto on triplets, an SM must also be Pareto on components and sub-Pareto on triplets and on components.

Pareto on components.—Proofs that the MinFlip and standard MRP SMs are Pareto on components in the consensus case have been given by Chen et al. (2003) and Bryant (2003), respectively. The split fit between a supertree and an input tree is the number of input tree full splits displayed by both. Split fit SM returns consensus trees that maximize the sum of the split fits across all input trees. Pareto splits are necessarily mutually compatible and compatible with every other combination of splits displayed by a set of input trees and must therefore be displayed by any supertree that displays the maximum number of input tree full splits. Thus, split fit is also Pareto on components (Pisani, 2002).

All liberal SMs except MinCut methods have objective functions based upon input tree-to-supertree distances (or similarities) that give an indication of the degree to which a supertree conflicts (or agrees) with the input trees (Thorley and Wilkinson, 2003). Optimal supertrees are defined as those that minimize (or maximize) the objective function. We define the cost of resolving input tree conflicts, C , as the absolute difference between the score of the supertree and the theoretically best possible score (i.e., the score if there were no input tree conflict). Thus, all known SMs that have an objective function minimize C .

A Pareto component P does not contribute to any conflicting relationships in the input trees. Any supertree that includes P will not differ from any input tree in that particular respect. Consequently, P can make no positive contribution to C for any candidate supertree that includes P , provided that only differences between displayed relationships of input trees and supertrees contribute to C . Of the methods that minimize C considered here, this holds for all but the average consen-

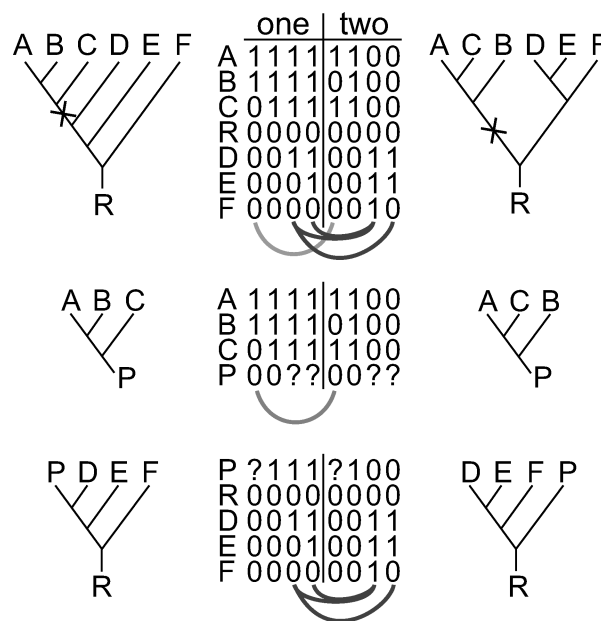


FIGURE A1. How a Pareto component (rooted full split) partitions the conflict between input trees into independent partitions. Shown at the top are two conflicting input trees that share the Pareto component (ABC)DEF (the rooted full split ABC|DEFR, where R is the root) and their corresponding component matrix representation. Below are the trees formed by cutting the edge corresponding to the Pareto component and relabeling it as P, where P can be understood as standing for the leaves in the other partition. For example, in the corresponding matrix representations, the question marks indicate conflicts (differences in the coding of the leaves from the other partition) that are irrelevant to the conflict within that partition. Lines linking matrix elements highlight the conflicts. In a path length matrix representation as used by the MSS method, distances involving P can, for example, be any of the original distances to a member of the other partition.

sus and average dendrogram, methods for which C can also reflect the additional cost of resolving differences in input tree branch lengths.

Cutting and relabeling the internal edges corresponding to P , as in Figure A1, partitions and preserves all the input tree conflicts. For an optimal supertree including P , C is the sum of the costs of the optimal resolutions of conflict within each of the partitions. Because the partitioned conflicts are independent, this combined cost cannot be bettered, for example, in any supertree that does not include P . But supertrees that do not include P incur an additional cost because they also conflict with the input trees with respect to P . Thus, C is minimized only by supertrees that include P (which must also be in the strict consensus of equally optimal supertrees).

This argument suggests, and leads us to conjecture, that all of the SMs considered here (including the consensus SMs of methods returning equally optimal supertrees), except perhaps the average dendrogram and average consensus, are Pareto and thus also sub-Pareto on components. However, there is as yet no proof of the independence of partitioned conflicts for irreversible and gene-tree parsimony methods or for the MSS, and these remain open problems. Bryant's (2003) proof that this holds in the case of standard MRP extends also to Purvis MRP and to triplet and quartet fit, which differ in the matrix representation but either employ or are equivalent to the same form of parsimony. Note that the strict consensus of all equally optimal supertrees of any SM that is Pareto on components will also include all Pareto components. No method is known to not be Pareto on components.

Co-Pareto on components.—Components displayed by one or more input trees are the only splits that can contribute to the maximization of the objective function of split fit supertrees. Thus, in the consensus case, a component that is incompatible with an input tree and not displayed by any input trees cannot be in a split fit supertree. Thus, when input

trees are binary, split fit is co-Pareto on components (Wilkinson et al., 2005a). When input trees have polytomies, an optimal split fit supertree could include arbitrary resolutions that do not contradict any displayed splits. In that case, split fit can fail to be co-Pareto (but not sub-Pareto) on components. In contrast, the corresponding strict consensus, the split fit* supertree, suppresses all arbitrary resolutions and must be co-Pareto on components. A method that is co-Pareto on components must also be co-Pareto (and sub-Pareto) on triplets and on nestings.

Our example confirms that triplet fit is not co-Pareto on components. For example, of the 1677 triplet MRP supertrees, 339 include the component (DE). This is not present in either input tree but all the triplets that it entails are present in at least one of the input trees. It also confirms that the MinCut methods are not co-Pareto on components

(Semple and Steel, 2000). For example, D and K are grouped together in the MinCut supertree (Fig. 1c) and D and K nest within A–P in both input trees but they are not a component in either input tree (Fig. 1).

Co-Pareto on triplets.—The triplet fit method is analogous to split fit, and by analogy we might expect that triplet fit* is co-Pareto and thus sub-Pareto on triplets, and that triplet fit is sub-Pareto on triplets and co-Pareto on triplets when input trees are binary (in which case there are no arbitrary resolutions). However, unlike full splits, combinations of displayed triplets can entail triplets that are not displayed. Thus, the analogy breaks down and there are, as yet, no proofs for any of these conjectures, which remain open problems. Similarly, quartet fit* is conjectured but has not been shown to be co-Pareto and sub-Pareto on quartets.

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Alarm Bells for the Molecular Clock? No Support for Ho et al.'s Model of Time-Dependent Molecular Rate Estimates

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In a recent paper, Ho et al. (2005) appear to have provided startling evidence for a relationship between the rate of molecular evolution and sampling time that they then describe with the fitting of vertically translated exponential decay curves. If correct, their results carry major implications for molecular evolutionary biology (Penny, 2005), and their work follows from the observed disparity between mitochondrial DNA (mtDNA) rate estimates directly measured from pedigree studies and those inferred from intraspecific and interspecific phylogenetic studies. A number of recent studies of control region mtDNA from detailed human pedigrees have reported exceptionally high estimates of mutation rate, summarized in Howell et al. (2003). Pooling data from two comparable Leber hereditary optic neuropathy studies (Howell et al., 1996, 2003), Howell et al. (2003) obtained a pedigree divergence rate of 1.0 mutations/bp/Myr (mutations per base pair per million years) for the control region. Building on these data, Howell et al. (2003) also combined data from a number of unrelated pedigree studies (Bendall et al., 1996; Cavelier et al., 2000; Heyer et al., 2001; Howell et al., 1996, 2003; Mumm et al., 1997; Parsons and Holland, 1998; Parsons et al., 1997; Sigurdardottir et al., 2000; Soodyall et al., 1997) and obtained a broadly similar control-region pedigree divergence rate of 0.95 mutations/bp/Myr. Ho et al. (2005) point out that this value is vastly greater (approximately 50×) than the phylogenetically derived divergence rate of approximately 0.02 mutations/bp/Myr for protein-coding mitochondrial DNA. However, it should be acknowledged that, as deduced from comparative

phylogenetic studies, the control region evolves much faster than the protein-coding regions within human mitochondrial DNA. Thus, in real terms, pedigree mutation rates for the human mitochondrial control region appear to be approximately 5- to 10-fold higher than phylogenetically derived divergence rates of 0.087 to 0.236 mutations/bp/Myr (Hasegawa et al., 1993; Stoneking et al., 1992; Tamura and Nei, 1993).

Although there are insufficient data to provide robust estimates on pedigree divergence rates for protein-coding regions of human mitochondrial DNA, Howell et al. (2003) have presented some suggestive data by pooling data from three studies (Cavelier et al., 2000; Howell et al., 1996, 2003), arriving at a divergence rate of 0.06 mutations/bp/Myr, approximately three times higher than the phylogenetic rate of 0.02 mutations/bp/Myr for protein-coding mitochondrial DNA (but note that Howell et al., 2003, incorrectly assert that the pedigree-derived estimate is approximately 30 times higher than the phylogenetic rate). Thus, bearing in mind the paucity of protein-coding pedigree data, current estimates place the mitochondrial DNA pedigree control region and protein-coding rates to be approximately 5 to 10 times and 3 times higher than their respective phylogenetic rates.

To investigate further the transition between pedigree mutation rates and long-term mutation rates, Ho et al. (2005) have estimated rates of change (c.f. rate of divergence) from mitochondrial sequences of primate (protein-coding and control region) and avian (protein-coding) taxa and compared these rates in the context of