

## MRP Supertree Construction in the Consensus Setting

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**ABSTRACT.** MRP supertree construction is an increasingly popular technique in the systematic biology community for combining phylogenetic information into a single output tree. It does so by combining source trees that are either fully or partially overlapping in terms of the leaf sets (the consensus and supertree settings, respectively). Although MRP supertree construction has strong parallels to true consensus techniques, its behaviour in the consensus setting is poorly known. I therefore use simulation to examine the behaviour of MRP supertree construction in this setting relative to several consensus techniques (strict, semi-strict, majority rule, and Adams-2 consensus) with well-documented properties. In reconstructing a known model tree, MRP supertree construction most closely resembles majority rule consensus in which other compatible groups are retained (fully resolved majority rule consensus). Both methods produce highly resolved output trees that were the most similar to the model tree, but also more likely to be incompatible with or contain clades not found on the model tree. Unlike fully resolved majority rule consensus, however, the MRP supertree may contain clades not found on any source tree. Finally, the MRP supertree always contains (i.e., is an equally or more resolved version of) the strict, semi-strict, and, in this study, 50% majority rule consensus trees of a given set of source trees.

### 1. Introduction

Supertree construction (*sensu* [4, 23]) represents a relatively new approach for combining phylogenetic information. Its key feature is the ability to construct a single, more inclusive output tree — the supertree — by combining source trees that may overlap only partially in their leaf sets. As such, it is distinct from consensus techniques, which are formally defined as being able to combine source trees with identical leaf sets only (following [15]). (I refer to the cases of source trees with partially versus fully overlapping leaf sets as the supertree and consensus settings, respectively.) The idea of a supertree was first formalized by Gordon [11], who provided a supertree equivalent of strict consensus (*sensu* [25]). Since that time, and especially in the past decade, Gordon's method has been refined and many new supertree techniques have been developed (see [4]).

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Strong parallels exist between supertree construction and consensus techniques, rooted in their common mechanism of combining a set of source tree topologies. Many supertree methods are merely the equivalent of well-established consensus techniques (e.g., strict and semi-strict consensus) adapted to the supertree setting. Supertree methods can also be used in the consensus setting (although the reverse is not true), presumably yielding identical results to their equivalent consensus techniques. Except for Bininda-Emonds and Sanderson [5], the behaviour of supertree methods in the consensus setting has not been examined in any detail. At best, only restricted examples have been looked at, largely to see how supertree methods perform in a simpler, more understandable setting.

In this paper, I use simulation to examine the behaviour of one supertree method, matrix representation with parsimony (MRP; [2, 20]), in the consensus setting. As a basis for comparison, I also examine several different consensus techniques with very different, but well-characterized properties. Altogether, this is done largely to further investigate how MRP combines trees. Although MRP is the most commonly used supertree method in the biological community, having been used to construct inclusive phylogenetic estimates of several large, diverse clades (see [4]), its properties remain poorly characterized.

## 2. Methods and materials

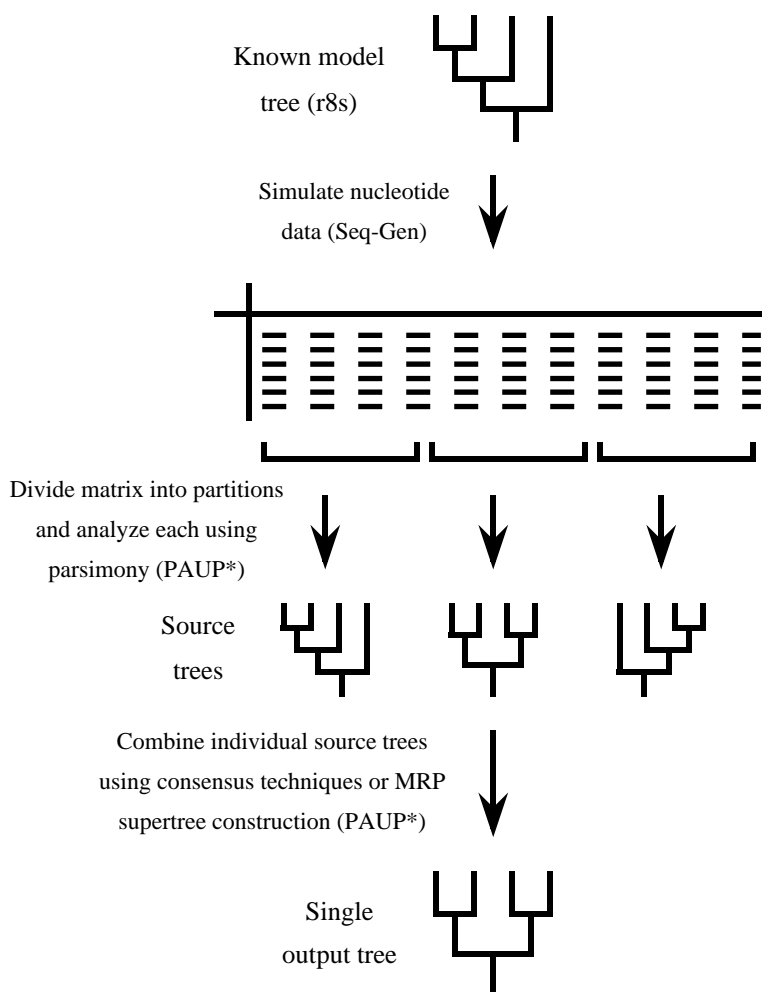
**2.1. Matrix representation with parsimony.** MRP uses matrix representation to encode the topology of a source tree into a series of matrix elements. Each informative internal vertex (“node”) is coded in turn. Taxa that are descended from the focal node are scored 1, all others receive 0. An all-zero outgroup is added to the matrix to polarize the elements. Analysis of the matrix using a parsimony criterion will recover the source tree exactly [18, 20].

In order to combine trees, the matrix representations of each source tree in a given set are combined into a single matrix. Taxa that are missing on a particular source tree, but are present on others in the set, are scored as missing (?) for that source tree. In the consensus setting, however, MRP will yield a binary matrix with no missing cells. An all-zero outgroup is again added to the combined matrix. The MRP supertree is typically taken to be the strict consensus of all the equally most parsimonious solutions (the MRP-spectrum; [29]).

Although it is the most popular of the current supertree methods, MRP has documented shortcomings and its suitability for combining trees has been questioned [16, 17, 26]. Restricted case studies show that the MRP supertree tends to be influenced most strongly by larger or less balanced source trees [3, 19, 30]. However, the impact of these biases seems to be minimal in practice. Elsewhere, I have demonstrated that MRP generally performs on a par with combining the primary data (“total evidence”; *sensu* [12]) under a wide range of conditions [5]. Moreover, the two methods show the same behaviour. Both become less accurate at reconstructing a known model tree as the number of source studies decreases, as the source studies possess more taxa or conflict with each other to a greater extent, and, in the supertree setting, as the source studies overlap to a lesser extent.

**2.2. Simulation protocol.** The basic protocol (see Figure 1) is similar to the one that I used elsewhere to test the performance of MRP in relation to total evidence [5]. Briefly, a known model tree was constructed according to a Yule branching process using r8s (available from <http://ginger.ucdavis.edu/r8s/>), with

branch lengths modeled so as to depart from the assumption of a molecular clock. Nucleotide sequences were then evolved along the model tree according to a standard Markov model using Seq-Gen v1.1 [21]. The resultant data set was subdivided into partitions of equal size (500 nucleotides each) according to the desired number of source trees. Each partition was analyzed individually using parsimony to produce single source trees. The parsimony analysis used PAUP\* v4.0b8 [28] and was weighted to correspond with the simulated model of molecular evolution as closely as possible. The set of source trees were then combined as an MRP supertree and using one of several different consensus techniques: strict [25], semi-strict (or combinable component; [7]), majority rule [14], and Adams-2 consensus [1]. In addition to a true 50% majority rule tree, a “fully resolved” majority rule consensus tree was calculated by including other groupings that were compatible with the 50% majority rule tree. All consensus trees were obtained using PAUP\*. For specific details concerning the preceding steps, please see Bininda-Emonds and Sanderson [5].



**Figure 1.** Diagrammatic representation of the simulation protocol. Where applicable, computer programs used for each step are given in parentheses.

I also investigated the effect of three variables on the performance of MRP or the consensus methods: the size of the source trees (8 or 32 taxa), the number of source trees (2 or 10), and the degree of incongruence among source trees (“low” or “high”). Source tree incongruence was modeled by altering the rate of evolution for the simulated sequence data in Seq-Gen; higher rates of evolution decrease the probability that the data partitions will yield similar source trees (see [5]). “Low” incongruence used an average rate of evolution of 0.1 substitutions per site measured along a path from the root to any tip of the tree, while “high” incongruence used 1.5. All possible combinations of these three variables were examined, with each set of simulated model parameters being replicated 100 times.

**2.3. Analysis and comparisons.** I performed two sets of comparisons. In the first, the topologies of both the MRP and consensus trees were compared to that of the model tree. In the second, the topologies of the different consensus trees were compared to the MRP supertree. All comparisons were made on unrooted trees using all combinations of the three variables above (source tree size, number, and incongruence). I used multivariate ANOVAs to determine whether there was a significant difference (with  $\alpha = 0.05$ ) between any of the methods or whether any of the individual variables were having a significant effect on the results.

Tree topologies were compared in two ways. First, overall similarity with the reference tree (i.e., model tree or MRP supertree) was calculated using either the consensus fork index (CFI; [9, 10]) or the partition metric ( $d_S$ ; [22]), respectively. My use of these different metrics is due to differences in the resolution of the reference trees (see [5]). Because the model tree is always binary (or “fully bifurcating”), any nodes in the test trees with more than two outgoing branches (“polytomies”) represent inaccuracies. This scenario is captured by CFI. In contrast, the MRP supertree may have polytomies, which should also appear in the test tree. In other words, polytomies are taken to be “hard” (see [13]), as is the case with  $d_S$ . Values of  $d_S$  were standardized for tree size by dividing through by  $2n - 6$ , where  $n$  = number of taxa [27] and subtracted from 1 to create a similarity metric equivalent to CFI.

I also compared the reference and test trees to see if they were compatible and, if so, whether one tree contained the other. By *compatible*, I mean that both trees contain the same clades or clades that resolve a polytomy in the other tree. If the two trees are compatible, but only one tree has clades that resolve polytomies in the second tree, then I define the former tree as *containing* the latter tree. Finally, I determined the number of clades for each tree that do not appear in the other tree. This was done without regard as to whether the *unique clades* contradicted clades found on the other tree or merely represented the resolution of a polytomy. The sum of the unique clades in both trees will equal the unstandardized value of  $d_S$  for those trees.

### 3. Results

**3.1. Comparisons with the model tree.** MRP showed the same behaviour in reconstructing the model tree as noted by Bininda-Emonds and Sanderson [5]: similarity to the model tree decreased significantly as source trees were fewer in number, contained more taxa, or conflicted with each other to a greater extent (Table 1). These same trends were also observed for the different consensus techniques, with two exceptions. First, the Adams, semi-strict, and especially strict

consensus trees were significantly less similar to the model tree with an increased number of source trees. Second, the amount of conflict between the source trees did not have a significant effect on either the Adams or strict consensus methods.

**Table 1.** Ability of MRP supertree construction and various consensus methods to reconstruct a known model tree. Values presented are mean values of CFI over 100 replicates; values in parentheses under each method represent the mean value over all factors for that method ( $n = 800$ ). MR = 50% majority rule consensus, either with (resolved) or without (50%) other compatible groups included.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
MRP	8	0.868	0.805	0.958	0.902
(0.848)	32	0.800	0.689	0.919	0.839
Adams	8	0.803	0.787	0.683	0.705
(0.687)	32	0.711	0.677	0.573	0.557
50% MR	8	0.800	0.775	0.895	0.843
(0.766)	32	0.690	0.634	0.785	0.708
Resolved MR	8	0.898	0.805	0.962	0.912
(0.875)	32	0.835	0.689	0.927	0.859
Semi-strict	8	0.863	0.798	0.727	0.705
(0.708)	32	0.787	0.661	0.612	0.510
Strict	8	0.800	0.775	0.655	0.685
(0.654)	32	0.690	0.634	0.508	0.488

These exceptions derive from Adams, semi-strict, and strict consensus being more sensitive to any (hard) conflict among the source trees. With a larger number of source trees, it is less likely that a given clade will be uncontradicted by all the source trees. Therefore, the output tree is “conservative”, with the more numerous polytomies it contains reducing its similarity to the completely resolved model tree (when measured using the CFI). For a similar reason, both semi-strict and strict consensus are less similar to the model tree with an increased number of taxa than are the remaining methods (Table 1).

All methods differed significantly in their ability to reconstruct the model tree (Table 1). Again, how conservative a method was had a large influence. Overall, the fully resolved majority rule consensus tree was the most similar (87.5%), followed by the MRP supertree (84.8%). The remaining consensus methods were noticeably less similar (< 77%), with both Adams and strict consensus being < 70% similar to the model tree on average.

It is also informative to examine the resolution of the various output trees and whether they are compatible with the model tree. Generally, the frequency of compatibility with the model tree decreased for all methods as the source trees were larger or contained more taxa, but increased (or was unaffected) with an increased number of source trees (Table 2). A clear difference in behaviour among the various methods was again apparent. MRP, Adams consensus, and especially fully resolved majority rule consensus were incompatible more frequently with the model tree, and

showed the largest decreases in frequency of compatibility. In contrast, the semi-strict and strict consensus trees were incompatible noticeably less often. With 10 source trees, these two methods produced consensus trees that were almost always compatible with the model tree.

This difference again generally derives from the trade-off between resolution (“conservativeness”) and similarity (Tables 3 and 4). Semi-strict and strict

**Table 2.** Number of replicates (out of 100) in which MRP supertree construction and various consensus trees yielded a tree that was compatible with the known model tree.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
MRP	8	80	63	80	64
	32	16	7	29	0
Adams	8	89	59	96	93
	32	31	8	77	40
50% MR	8	97	72	96	84
	32	79	37	96	58
Resolved MR	8	61	40	78	58
	32	2	1	17	0
Semi-strict	8	82	66	99	96
	32	22	25	99	94
Strict	8	97	72	100	97
	32	79	37	100	97

**Table 3.** Resolution of MRP supertree and various consensus trees when reconstructing a known model tree. Values presented are the mean proportion of clades present compared to a fully bifurcating tree over 100 replicates; values in parentheses under each method represent the mean value over all factors.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
MRP	8	0.905	0.877	0.992	0.980
	(0.921)	32	0.878	0.815	0.967
Adams	8	0.822	0.862	0.690	0.717
	(0.724)	32	0.749	0.784	0.582
50% MR	8	0.805	0.823	0.902	0.872
	(0.785)	32	0.698	0.664	0.786
Resolved MR	8	0.980	0.877	1.000	1.000
	(0.991)	32	0.963	0.815	0.999
Semi-strict	8	0.893	0.863	0.728	0.712
	(0.735)	32	0.839	0.719	0.613
Strict	8	0.805	0.823	0.655	0.690
	(0.667)	32	0.698	0.664	0.508

**Table 4.** Proportion of clades found on either the known model tree (A) or on an MRP supertree or various consensus methods estimates of it (B) that are not found on the other tree (“unique clades”). Values presented are mean proportions over 100 replicates; values in parentheses under each method represent the mean value over all factors.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
A)					
MRP	8	0.132	0.195	0.042	0.098
(0.152)	32	0.200	0.311	0.081	0.161
Adams	8	0.197	0.213	0.317	0.295
(0.313)	32	0.289	0.323	0.427	0.443
50% MR	8	0.200	0.225	0.105	0.157
(0.234)	32	0.310	0.366	0.215	0.292
Resolved MR	8	0.102	0.195	0.038	0.088
(0.125)	32	0.165	0.311	0.073	0.141
Semi-strict	8	0.137	0.202	0.273	0.295
(0.292)	32	0.213	0.339	0.388	0.490
Strict	8	0.200	0.225	0.345	0.315
(0.346)	32	0.310	0.366	0.492	0.512
B)					
MRP	8	0.039	0.082	0.034	0.080
(0.080)	32	0.087	0.150	0.050	0.118
Adams	8	0.022	0.090	0.011	0.017
(0.050)	32	0.050	0.136	0.015	0.056
50% MR	8	0.005	0.059	0.007	0.031
(0.023)	32	0.010	0.045	0.002	0.026
Resolved MR	8	0.083	0.082	0.038	0.088
(0.117)	32	0.132	0.150	0.072	0.140
Semi-strict	8	0.032	0.075	0.002	0.010
(0.033)	32	0.062	0.076	0.001	0.004
Strict	8	0.005	0.059	0.000	0.008
(0.016)	32	0.010	0.045	0.000	0.002

consensus produce the most poorly resolved trees. On average, resolution was < 75% compared to a fully bifurcating solution, but often around 50% with 10 source trees (Table 3). But, semi-strict and strict consensus rarely inferred clades that were not found on the model tree (< 3.5% of clades), whereas about 30% of the clades on the model tree were not found on these consensus trees (Table 4). In contrast, the MRP and fully resolved majority rule trees were on average better resolved (> 92%) and in a sense more similar to the model tree (< 16% of the clades on the model tree were unique). But, this increased resolution comes at the cost of inferring more unique clades (> 8.0%) than did the semi-strict and strict consensus.

### 3.2. Comparisons between the MRP supertree and consensus trees.

Similarity between the consensus trees and MRP supertree on average decreased

slightly, but significantly as the source trees increased in size or number (Table 5). This latter trend was particularly strong for strict consensus, whereas fully resolved majority rule consensus yielded a tree that was slightly more similar to the MRP supertree as the number of source trees increased. Similarity to the MRP supertree also decreased slightly, but significantly with an increase in the amount of conflict between the source trees for all methods except Adams and 50% majority rule consensus. These trends agree with expectations. All three cases (i.e., larger, more numerous, or more conflicting source trees) increase the probability that the respective trees will differ, either on probabilistic grounds (larger or more numerous source trees) and/or because of how the different methods combine trees (more conflicting source trees).

The different consensus methods all differed significantly in their similarity to the MRP supertree (Table 5). The most similar tree was that produced by fully resolved majority rule consensus, followed by 50% majority rule and finally the more conservative consensus methods. Despite the semi-strict and strict consensus trees being the least similar to the MRP supertree, the MRP supertree was always compatible with and at least as equally resolved as these trees (i.e., the supertree *resolves* each consensus tree; Table 6). This is in accordance with the proof of Bryant [8] and was also true of the MRP supertree and the 50% majority rule consensus tree. However, the latter observation pertains to this study only, and need not always be true [8]. The MRP supertree was significantly more resolved than the tree produced by each of these three consensus methods (> 13%, on average; Table 3), which is reflected in the large number of unique clades that it possessed in relation to each consensus tree (between 14 and 27%; Table 7). In contrast, the three consensus methods never yielded clades that were not also found on the supertree (Table 7).

**Table 5.** Similarity of various consensus trees to the MRP supertree when reconstructing a known model tree. Values presented are mean values of  $d_S$  (standardized for tree size and subtracted from 1) over 100 replicates; values in parentheses under each method represent the mean value over all factors.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
Adams	8	0.934	0.953	0.811	0.832
(0.687)	32	0.898	0.888	0.790	0.779
50% MR	8	0.940	0.968	0.946	0.935
(0.766)	32	0.907	0.922	0.907	0.884
Resolved MR	8	0.951	0.926	0.993	0.982
(0.875)	32	0.935	0.854	0.977	0.939
Semi-strict	8	0.993	0.992	0.842	0.839
(0.708)	32	0.980	0.950	0.817	0.772
Strict	8	0.940	0.968	0.798	0.826
(0.654)	32	0.907	0.922	0.763	0.761



**Table 6.** Number of replicates (out of 100) in which various consensus methods yielded a tree that was compatible with the MRP supertree when reconstructing a known model tree.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
Adams	8	99	98	96	96
	32	79	53	74	46
50% MR	8	100	100	100	100
	32	100	100	100	100
Resolved MR	8	99	100	99	98
	32	78	45	88	51
Semi-strict	8	100	100	100	100
	32	100	100	100	100
Strict	8	100	100	100	100
	32	100	100	100	100

**Table 7.** Proportion of clades found on either the MRP supertree (A) or on various consensus methods (B) that are not found on the other tree (“unique clades”) when reconstructing a known model tree. Values presented are mean proportions over 100 replicates; values in parentheses under each method represent the mean value over all factors.

Method	Number of taxa	Number of source trees			
		2		10	
		Degree of conflict		Degree of conflict	
		low	high	low	high
A)					
Adams	8	0.102	0.049	0.311	0.276
	(0.236) 32	0.185	0.144	0.409	0.414
50% MR	8	0.106	0.057	0.091	0.110
	(0.146) 32	0.204	0.177	0.187	0.236
Resolved MR	8	0.003	0.000	0.002	0.006
	(0.018) 32	0.022	0.067	0.007	0.038
Semi-strict	8	0.012	0.015	0.265	0.272
	(0.194) 32	0.043	0.115	0.366	0.462
Strict	8	0.106	0.057	0.339	0.294
	(0.267) 32	0.204	0.177	0.475	0.486
B)					
Adams	8	0.017	0.040	0.011	0.013
	(0.040) 32	0.047	0.119	0.018	0.056
50% MR	8	0.000	0.000	0.000	0.000
	(0.000) 32	0.000	0.000	0.000	0.000
Resolved MR	8	0.079	0.123	0.010	0.025
	(0.087) 32	0.109	0.231	0.039	0.082
Semi-strict	8	0.000	0.000	0.000	0.000
	(0.000) 32	0.000	0.000	0.000	0.000
Strict	8	0.000	0.000	0.000	0.000
	(0.000) 32	0.000	0.000	0.000	0.000

The MRP supertree was frequently compatible with the Adams and fully resolved majority rule consensus trees with source trees of eight taxa ( $> 96\%$  of the time; Table 6). This was true regardless of the number of source trees or how much conflict there was between them. Both the MRP supertree and consensus trees contained unique clades not found on the other tree (Table 7). The supertree contained more unique clades than did the Adams consensus tree (12.0 versus 5.6%, respectively), but fewer than the fully resolved majority rule tree (2.3 versus 13.6%, respectively). Compatibility frequency decreased noticeably with larger source trees (32 taxa) to between 50 and 90%, with the differential effects of source tree conflict and number of source trees becoming apparent. At high levels of conflict, the MRP supertree was only compatible with either the Adams or fully resolved majority rule tree about 50% of the time. Increasing the number of source trees decreased the frequency of compatibility between the MRP supertree and Adams consensus tree, but increased it between the supertree and fully resolved consensus tree (Table 6). Again, the MRP supertree contained many more unique clades than did the Adams consensus tree (35.2 versus 2.5%, respectively), but about the same low number as the fully resolved majority rule consensus tree (1.3 versus 3.9%, respectively; Table 7).

#### 4. Discussion

Despite much research, the properties of MRP supertree construction remain somewhat obscure. In particular, there is no obvious relationship between the clades that appear on the MRP supertree and some property of theirs in the set of source trees. This is in sharp contrast to the consensus methods examined herein, where clear, informative statements are possible. For instance, the clades in a strict consensus tree are found in all source trees, those in a semi-strict tree are not contradicted by any source tree, those in the majority rule trees are found in  $> 50\%$  of the source trees (or are compatible with these clades), and those in an Adams tree represent nestings (i.e., subclades that appear within a more inclusive clade) found in all source trees.

At best, it can be said that the MRP supertree is the most parsimonious summary of the hierarchical clustering information present in a set of source trees [3]. However, this reveals comparatively little information about the individual clades on the supertree. This shortcoming on the part of MRP derives from the intervening parsimony analysis, in which the matrix elements can interact and be influenced by reversals and other forms of homoplasy if the source trees conflict with one another [3]. However, many other supertree methods do allow clear statements of the clades they recover. For example, Gordon's [11] strict supertree method and its generalization as MinCutSupertrees [24] to combine incompatible source trees are the functional equivalents of strict and Adams consensus, respectively. As such, supertrees derived using these two methods display relationships and clusters, respectively, that are present on all source trees.

Nonetheless, this study does provide some insight into the mechanics of MRP supertree construction, at least in the consensus setting. In many ways, MRP resembles the fully resolved majority rule consensus method. Both methods produce highly resolved trees that are the most similar to the model tree, albeit at the costs of inferring a greater proportion of clades that are not found on the model tree and more frequent incompatibility with the model tree. However, the two methods do

not produce identical trees. Furthermore, because the empirical data in this study show that MRP supertree often contains the 50% majority rule consensus tree, we know that many of the clades in the MRP supertree appear in more than 50% of the source trees. Similarly, a smaller number of clades appear in all source trees since the MRP supertree contains the strict consensus tree. Unfortunately, these clades cannot easily be distinguished from the other less well-supported or even spurious clades. Unlike all consensus techniques except Adams consensus, MRP supertrees can contain “novel clades” that do not appear in any source tree or may even be contradicted by every source tree [3]. It may be possible to distinguish such novel clades, however, using support measures such as Bremer’s decay index [6] obtained for the MRP supertree.

Although it can be used in the consensus setting, MRP possesses two distinct shortcomings to existing (true) consensus techniques. The first, as mentioned, is the inability to relate clades on the MRP supertree with some property of theirs in the set of source trees. The second and more important perhaps, is the computational complexity of the MRP analysis. In particular, the parsimony step is NP-hard, meaning that it may not have an efficient solution. Although the use of heuristic search strategies will improve analysis times, they do so at the cost of not being able to guarantee finding all optimal solutions. This situation is in contrast to most of the consensus techniques examined herein, which possess efficient polynomial time algorithms. The MRP analysis has an efficient solution only in the unlikely event that the source trees do not conflict with one another. However, even in such situations, it may be preferable to use Gordon’s [11] strict supertree method, which is equivalent to MRP supertree construction under these conditions [29] and does not require enumeration of the MRP-spectrum [4]. For these reasons, MRP supertree construction is perhaps best suited to be used in the supertree setting only.

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