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Phylogenetic supertrees: assembling the trees of life

Michael J. Sanderson, Andy Purvis and Chris Henze

Despite the recent explosive growth in phylogenetics, the number of species included in phylogenies to date is still an insignificant fraction of biodiversity. Moreover, most individual studies sample only a few taxa (usually under 50), so that our current understanding of the tree of life is fragmentary. More inclusive phylogenetic hypotheses are highly desirable: systematists wish to be as comprehensive as possible in making statements about phylogenetic relationships, and comparative biologists often study sets of taxa that do not correspond neatly to sets found on available phylogenies, so are forced to cobble together disparate phylogenies[1–3] into a single tree. Any such tree containing all the taxa from a collection of trees is a 'supertree' in the broad sense (Box 1). An ideal supertree, which we term a 'strict supertree', is one that agrees with all the trees from which it was derived.

The obvious approach for combining analyses is simply to combine the original data matrices into a single larger matrix, inserting question

Systematists and comparative biologists commonly want to make statements about relationships among taxa that have never been collectively included in any single phylogenetic analysis. Construction of phylogenetic 'supertrees' provides one solution. Supertrees are estimates of phylogeny assembled from sets of smaller estimates (source trees) sharing some but not necessarily all their taxa in common. If certain conditions are met, supertrees can retain all or most of the information from the source trees and also make novel statements about relationships of taxa that do not co-occur on any one source tree. Supertrees have commonly been constructed using subjective and informal approaches, but several explicit approaches have recently been proposed.

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marks in cells where taxa from one analysis have not been scored in another[4] (Fig. 1). This 'supermatrix' approach has the advantage that the information retained in individual characters can help sort out relative strengths and weaknesses within and between the different data sets[5], which is philosophically in keeping with the so-called 'total evidence' approach to combining phylogenetic information[6].
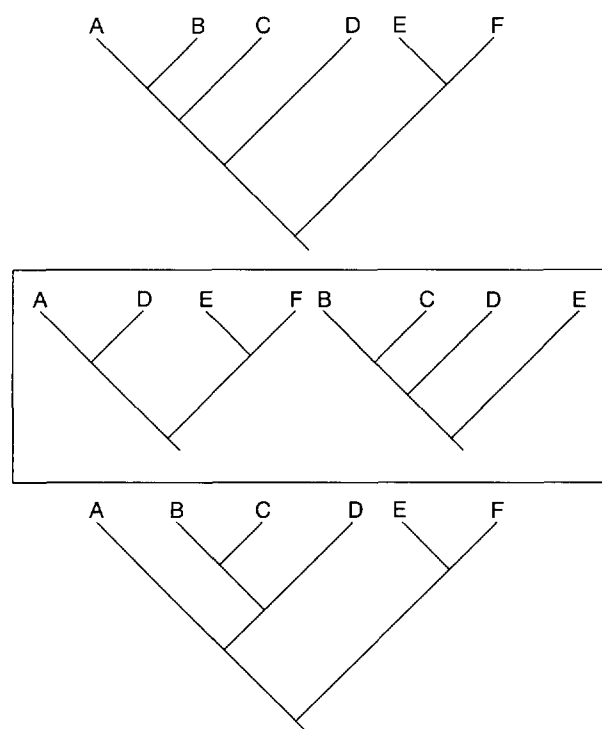
However, as a long-term strategy for assembling ever larger phylogenies, reliance on the construction of a character supermatrix is untenable. If only a few taxa are common between data sets, most of the newly combined data matrix will be scored as question marks. Gathering the new data needed to fill in the gaps would require exorbitant investments of resources. Other drawbacks of the supermatrix approach are that some data sets (e.g. from DNA–DNA hybridization) cannot be included, and that construction of initial hypotheses of homology and/or alignment becomes ever more difficult as the matrix grows.

Box 1. Supertree terminology

The trees that will be used to construct the supertree are the **source** trees. For the purposes of this article, all trees will be considered rooted (see Ref. 14 for discussion of the unrooted case). Taxa found on only one source tree are **unique**; those found on two or more are **shared**. Any tree containing all the taxa found among the source trees is a **supertree**. Two additional concepts are needed to define a **strict supertree**. Tree A is **consistent** with tree B if, when we consider only their shared taxa, tree B is the same as tree A or can be derived from tree A by collapsing one or more of A's branches[14]. If there exists a tree S that is consistent with each source tree and also contains all their taxa (shared and unique), then the source trees are **compatible**, and S is a **strict supertree** of the set.

Two compatible source trees (boxed) are shown below, together with two strict supertrees that are consistent with them, despite disagreeing with each other (the set of strict supertrees can itself be characterized by consensus methods[28]). Novel statements about relationships can be made from the supertree that were not possible based on the source trees alone, such as that taxa B and C are more closely related to each other than either is to F.

Box 2. Construction of supertrees by Matrix Representation with Parsimony (MRP)

In MRP a new matrix is constructed whose characters refer to the topologies of the source trees. Each clade (node) on a source tree yields one character in the matrix (see hypothetical example below). Two schemes have been proposed for determining which taxa are scored as '0', '1', or '?'. Baum[9] and Ragan[5] score a '1' for each taxon in the clade, a '0' for each taxon not in the clade, and a '?' for taxa not present in that source tree. Purvis's[10] method differs in that only the sister group of the clade is given a '0': more distant relatives (as well as those not present in the source tree) are given '?'. In the example below, the boxed cells show differences between the two procedures. Parsimony analysis of the characters derived from a single source tree will regenerate that tree, whichever procedure is adopted. The characters from all source trees are then combined into one matrix and analysed with parsimony. The trees should be rooted assuming a hypothetical ancestor having states with all '0s'. The two coding schemes differ in how they weight trees of different sizes[11]: one tries to give trees the same weight regardless of size[10], whereas the other[5,9] effectively treats some clades in large trees as being very well supported by virtue of being highly nested (and consequently supported by many 1s).

How much do these differences matter? Using a diverse collection of 112 source trees of primates, Purvis and Webster[31] constructed supertrees using each coding method in turn. With Purvis's[10] method, the supertree tree resolves 160 nodes (out of a possible 202); all but 12 of these are still present when source trees are coded according to Baum[9] and Ragan[5]. None of the nodes absent from the latter analysis is strongly supported in the former (assayed by bootstrap methods[31]). These results imply that the two methods generally agree in their strongly-held opinions, but disagree more as conflict among source trees increases.

Ronquist[11] points out that Purvis's[10] coding procedure fails to weight source trees equally, and favors a different modification whereby characters from each source tree are weighted according to the number of taxa the tree contains. However, this also fails to weight source trees equally[26]. The effect of these weighting choices may be less important than the effect of weighting clades by relative character support, which can vary greatly among clades.

Baum, Ragan coding scheme

A	1	1	1	....	0	0
B	1	1	1	....	1	0
C	0	1	1	....	?	?
D	0	0	1	....	?	?
E	0	0	0	....	?	?
F	?	?	?	....	1	1
G	?	?	?	....	1	1

Purvis coding scheme

A	1	1	1	....	0	[?]
B	1	1	1	....	1	0
C	0	1	1	....	?	?
D	[?]	0	1	....	?	?
E	[?]	[?]	0	....	?	?
F	?	?	?	....	1	1
G	?	?	?	....	1	1

	Sequence 1	Sequence 2
Taxa	1234.......	1234.......
A	aaccgtgtcagg	????????????
B	aaccacatcaaa	????????????
C	aaccgtgtcaaa	????????????
D	atttttgtcaaa	aaccgtgtcaaa
E	aaccgtgtcaga	aaccctgtcaaa
F	????????????	aaccccgtcaca
G	????????????	aaccgggtcaaa
H	????????????	acccgtgtcaaa

Fig. 1. 'Supermatrix' approach for construction of supertrees via combination of source data sets ('total evidence'). Taxa A–E have been scored for all characters in sequence 1. Taxa D–H have been scored for sequence 2. Only taxa D and E have data for both sequences. All other cells of the matrix are scored as 'missing' ('?'). Following combination of the data, the matrix is handled by standard phylogenetic parsimony analysis.

Alternatives to the supermatrix approach include replacing species-rich clades with a few exemplar taxa, and 'compartmentalization'[7], in which the hypothetical ancestors of major clades are first reconstructed and then used as terminal taxa in a higher level analysis. As yet these methods are still somewhat *ad hoc*; no general algorithms have been implemented.

Algorithms for constructing supertrees

An option for which explicit algorithms do exist is to combine the trees (rather than the data) resulting from multiple phylogenetic studies, in a manner akin to meta-analysis[8]. Two basic algorithms (along with several variations) have been proposed for constructing supertrees.

The MRP (for Matrix Representation with Parsimony) method (Box 2) can be used whether or not the source trees are compatible[5,9–11]. The method converts the topology of each source tree into an equivalent data-matrix representation. These matrices are then combined, with question marks used appropriately for unique taxa: the supertrees are then the set of most parsimonious trees for this new matrix.

If source trees are compatible, strict supertrees can be constructed by much more direct algorithms (Box 3), but the problem is still not trivial[12–16]. Although an efficient general solution for finding *one* supertree for an arbitrary set of source trees has been available for some time[12], as has an intuitively understandable algorithm that works for a pair of source trees[13] (Box 3), the general problem of characterizing the set of *all* supertrees for *any* number of source trees has only recently been solved[14,16].

Figure 2 shows an example of supertree construction for the more typical case in which source trees are incompatible.

For some purposes, it is desirable to incorporate information about branch lengths (expected amounts of character change) into the supertree. For example, a supertree derived from source trees taken from several genes could be used to estimate average numbers of substitutions, even for taxa not shared by all source trees. Few results are available in this problem, but Lapointe and Cucumel[17] advocate the average consensus procedure, which minimizes the 'distance' from the consensus (supertree) to all the source trees. This method uses a matrix of summed branch lengths, and estimates missing entries in the matrix that arise from nonshared taxa by invoking assumptions that the matrix is additive or ultrametric[18].

Advantages and limitations

Strict supertree construction is conservative: the result cannot conflict with *any* phylogenetic relationships in *any* source tree. However, it applies only when source trees are compatible. Conflict among source trees may be common, becoming more likely as the numbers of source trees or shared taxa increases. MRP handles conflict essentially by weighing the evidence in different source trees, without any tree having the power of veto. We discuss below how source trees, or the statements of relationships they make, might be weighted according to their relative reliability. It might also be useful to modify the strict algorithm, which is quite fast, to handle incompatible source trees. This could be accomplished by (1) treating the conflicts with consensus methods before application of the strict algorithm, and (2) selective removal of problematic shared taxa until the remaining subtrees are compatible[13,14].

One difference between the two methods is important for those interested in using supertrees to perform quantitative evolutionary or ecological analyses (such as the 'comparative method'[19]). The strict supertree method produces only a *consensus* of the strict supertrees: one cannot enumerate all the supertrees given the strict consensus supertree (merely finding all resolutions of polytomies might generate trees that are not strict supertrees). This matters because comparative tests perform best when the estimate of phylogeny on which they are based is as fully resolved as the real tree[20–24]. If it is not, methods either become unwieldy to apply[22], lose statistical validity[21,22], or lose power[23,24]. MRP yields a set of supertrees first, before their strict consensus is computed: all or some of these true supertrees could be used for comparative analyses.

Another difference between methods is that strict supertree construction may be much faster than MRP. Construc-

Box 3. Construction of supertrees by the strict supertree algorithm

Strict supertree construction can be understood readily in the case of two source trees[13] as shown in the illustrations below. Trees (a) and (b) share three taxa (boxed) in common. First, a 'backbone' tree (c) is constructed using just those shared taxa. Next, each branch of the backbone tree is examined relative to the corresponding branch(es) in the source trees. There are three possibilities: (1) neither source tree has unique taxa attached to the corresponding backbone branch (denoted by '_,_') – in that case, do nothing and continue to the next branch of the backbone tree; (2) both source trees have unique taxa attached to that branch (denoted by 'X,Y') – in that case, all the unique taxa are attached to the backbone tree at a new unresolved (collapsed) node – see tree (d); or (3) only one tree has unique taxa along that branch (denoted by 'X,_') – in that case preserve the subtree from the tree having unique taxa and copy it to the backbone tree – see tree (d). The resulting tree is the strict consensus of all 'strict supertrees' consistent with the source trees (note that other consensus techniques may preserve more information from the supertrees than strict consensus does[32,33]). For more than two source trees, this algorithm depends on the order of input, and a more elaborate algorithm described by Steel[14] must be used.
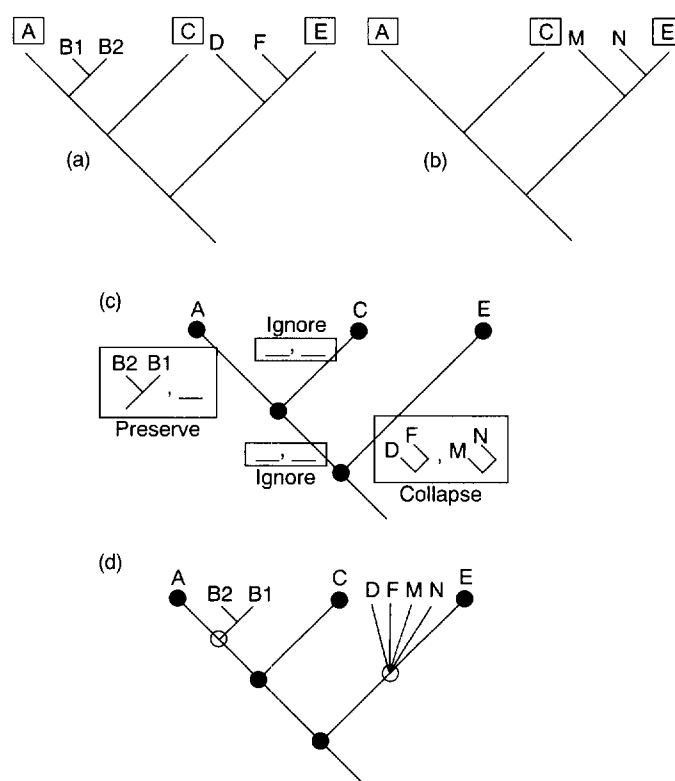
tion of supertrees by MRP (Box 2) is computationally intense because it uses parsimony methods that can require an 'exponential' amount of computer time[25]. The strict supertree algorithms (Box 3), on the other hand, require merely 'polynomial time', to finish[12–14,16]. MRP is most likely to struggle if there are many consistent supertrees, which is equivalent to uncovering a large number of equally parsimonious trees from the MRP matrix. Parsimony programs may fail to find all trees because of shortcuts in their heuristic search strategies (multiple searches with random addition sequences may help), or they may simply take too long to be practical.

Ambiguity, support and weighting

If source trees are mutually compatible then the issue of the relative support of different trees is moot: no relationships strongly supported by 'good data' from one source tree will be contradicted by 'bad data' from another source tree, and the signal in each data set will be seen in the supertree(s). When
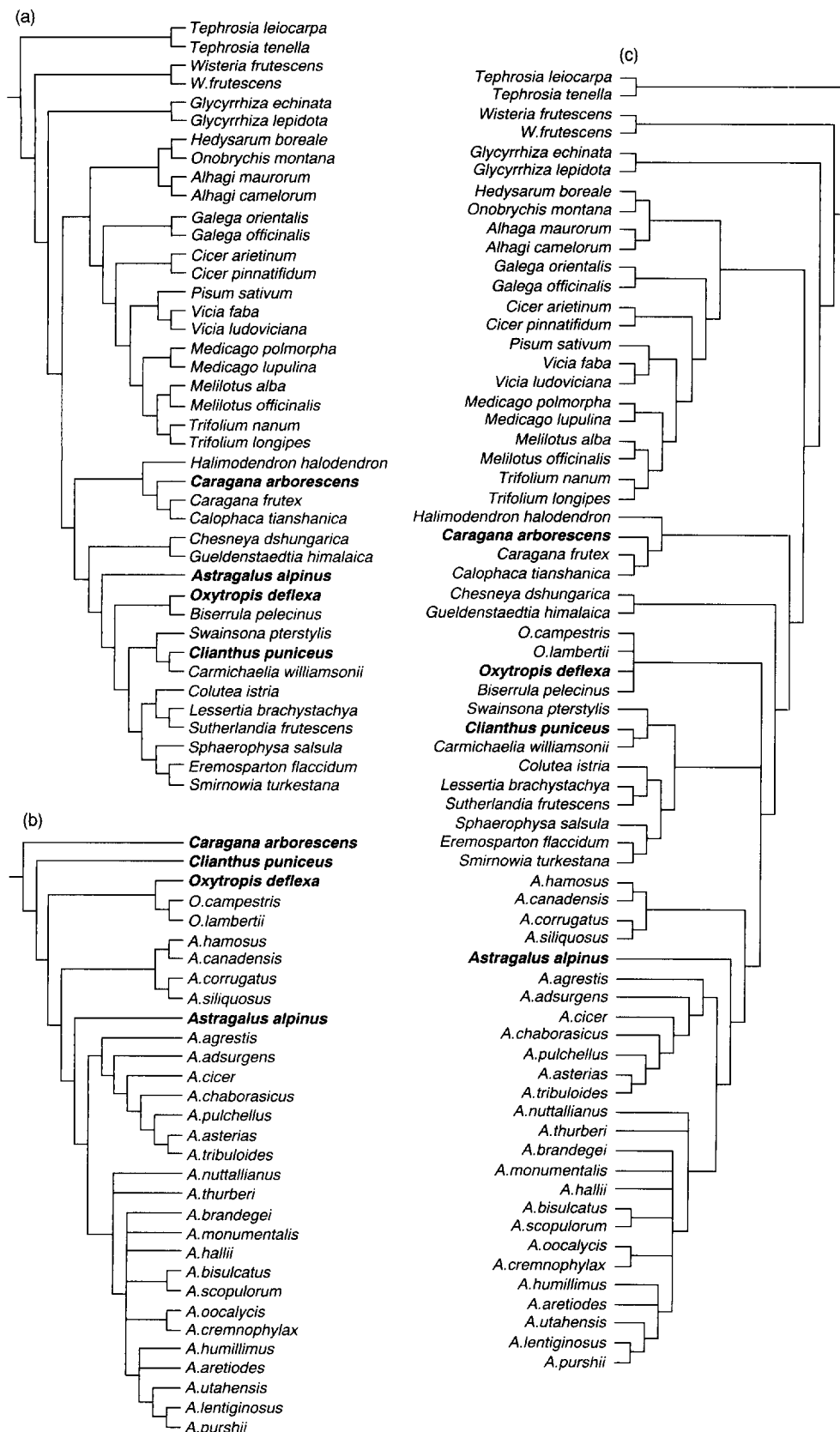
(a)

```
┌─ Tephrosia leiocarpa
└─ Tephrosia tenella
┌─ Wisteria frutescens
└─ W.frutescens
┌─ Glycyrrhiza echinata
└─ Glycyrrhiza lepidota
┌─ Hedysarum boreale
└─ Onobrychis montana
┌─ Alhagi maurorum
└─ Alhagi camelorum
┌─ Galega orientalis
└─ Galega officinalis
┌─ Cicer arietinum
└─ Cicer pinnatifidum
┌─ Pisum sativum
├─ Vicia faba
└─ Vicia ludoviciana
┌─ Medicago polmorpha
└─ Medicago lupulina
┌─ Melilotus alba
└─ Melilotus officinalis
┌─ Trifolium nanum
└─ Trifolium longipes
─ Halimodendron halodendron
┌─ Caragana arborescens
├─ Caragana frutex
└─ Calophaca tianshanica
┌─ Chesneya dshungarica
└─ Gueldenstaedtia himalaica
─ Astragalus alpinus
┌─ Oxytropis deflexa
└─ Biserrula pelecinus
┌─ Swainsona pterstylis
┌─ Clianthus puniceus
└─ Carmichaelia williamsonii
┌─ Colutea istria
┌─ Lessertia brachystachya
└─ Sutherlandia frutescens
┌─ Sphaerophysa salsula
┌─ Eremosparton flaccidum
└─ Smirnowia turkestana
```

(b)

```
┌─ Caragana arborescens
├─ Clianthus puniceus
├─ Oxytropis deflexa
┌─ O.campestris
└─ O.lambertii
┌─ A.hamosus
└─ A.canadensis
┌─ A.corrugatus
└─ A.siliquosus
─ Astragalus alpinus
┌─ A.agrestis
├─ A.adsurgens
├─ A.cicer
├─ A.chaborasicus
┌─ A.pulchellus
├─ A.asterias
└─ A.tribuloides
─ A.nuttallianus
─ A.thurberi
┌─ A.brandegei
├─ A.monumentalis
├─ A.hallii
┌─ A.bisulcatus
└─ A.scopulorum
┌─ A.oocalycis
└─ A.cremnophylax
─ A.humillimus
├─ A.aretiodes
├─ A.utahensis
┌─ A.lentiginosus
└─ A.purshii
```

(c)

```
Tephrosia leiocarpa ┐
Tephrosia tenella ┘
Wisteria frutescens ┐
W.frutescens ┘
Glycyrrhiza echinata ┐
Glycyrrhiza lepidota ┘
Hedysarum boreale ┐
Onobrychis montana ┘
Alhaga maurorum ┐
Alhagi camelorum ┘
Galega orientalis ┐
Galega officinalis ┘
Cicer arietinum ┐
Cicer pinnatifidum ┘
Pisum sativum ┐
Vicia faba ┐
Vicia ludoviciana ┘
Medicago polmorpha ┐
Medicago lupulina ┘
Melilotus alba ┐
Melilotus officinalis ┘
Trifolium nanum ┐
Trifolium longipes ┘
Halimodendron halodendron ─
Caragana arborescens ┐
Caragana frutex ┐
Calophaca tianshanica ┘
Chesneya dshungarica ┐
Gueldenstaedtia himalaica ┘
O.campestris ┐
O.lambertii ┘
Oxytropis deflexa ─
Biserrula pelecinus ┘
Swainsona pterstylis ─
Clianthus puniceus ┐
Carmichaelia williamsonii ┘
Colutea istria ─
Lessertia brachystachya ┐
Sutherlandia frutescens ┘
Sphaerophysa salsula ─
Eremosparton flaccidum ┐
Smirnowia turkestana ┘
A.hamosus ┐
A.canadensis ┘
A.corrugatus ┐
A.siliquosus ┘
Astragalus alpinus ─
A.agrestis ─
A.adsurgens ─
A.cicer ─
A.chaborasicus ─
A.pulchellus ┐
A.asterias ┐
A.tribuloides ┘
A.nuttallianus ─
A.thurberi ─
A.brandegei ─
A.monumentalis ─
A.hallii ─
A.bisulcatus ┐
A.scopulorum ┘
A.oocalycis ┐
A.cremnophylax ┘
A.humillimus ─
A.aretiodes ─
A.utahensis ─
A.lentiginosus ┐
A.purshii ┘
```

Fig. 2. Supertree constructed from two molecular phylogenies of legumes, one (a) sampling genera related to the genus *Astragalus*[28], and the other (b) concentrating on species within *Astragalus*[29]. The source trees share four species in common (in boldface), but the topologies of these shared taxa differ with respect to the position of *Oxytropis deflexa* (i.e. they are incompatible – see Box 1). (c) However, the consensus of supertrees can still be constructed by the MRP method, which produces a highly resolved tree with a polytomy indicating uncertain relationship of *Oxytropis deflexa* (and other *Oxytropis* species) to related genera.

source trees conflict, on the other hand, supertree algorithms may resolve these conflicts in unexpected ways[10,11]. Several authors have suggested the desirability of weighting the contributions of individual trees to the final results. This can be accomplished under MRP by weighting characters in the new MRP matrix. If an entire source tree is thought more reliable than others, for example, then all the characters derived from it could be given more weight. Within a source tree, characters can be weighted according to the degree of support (e.g. decay index, bootstrap score) for the corresponding nodes. Differential weighting will often be reasonable, although no scheme yet proposed always weights source trees equally[26].

An extreme but defensible version of the 'weight and see' policy is to pare source trees down to their well-supported statements before combining them[15]. Robust statements from different source trees are much less likely to conflict. This approach discards the information most likely to mislead, broadens the applicability of direct supertree construction and helps circumvent questions of how to code and weight source trees in MRP. Some conflict may still remain: significant discrepancies among source trees may reflect different phylogenetic histories of the genes or organisms involved, which may merit further investigation. In such cases it is inappropriate to construct supertrees; instead some method of 'reconciling' the source trees (i.e. mapping one onto another) is a more illustrative procedure[27].

Identifying candidates for supertree construction: tree-graphs

Phylogenies based on many different kinds of data and analysis are rapidly becoming available. Such phylogenies are candidate source trees for the construction of supertrees. In the context of the vast number of trees now in the literature, it is difficult to identify sets of trees that could be input to supertree procedures. One useful heuristic device is a

so-called 'tree-graph,' such as that shown in Fig. 3. A tree-graph is a graph in which each node represents a phylo-genetic tree from some analysis. Two nodes are connected in this graph if and only if they share at least two taxa in com-mon, the minimum requirement for supertree construction.

The tree-graph in Fig. 3 shows the phylogenetic trees currently in the TreeBASE database (herbaria.harvard.edu/treebase). In this graph there are connected components, or 'islands' of trees, that are isolated from other islands. Trees within an island are candidates for supertree construction. Trees in different islands are not. Were such a tree-graph available for all phylogenetic studies, candidates for supertree construction would be readily identifiable. Tree-graphs such as that in Fig. 3 may pave the way to the eventual assembly of progressively more inclusive phylogenies from large numbers of partially overlapping smaller trees. In the meantime, supertrees will at least allow comparative biologists to under-take synthetic analyses that transcend the limited taxonomic sampling found in any one phylogenetic study.
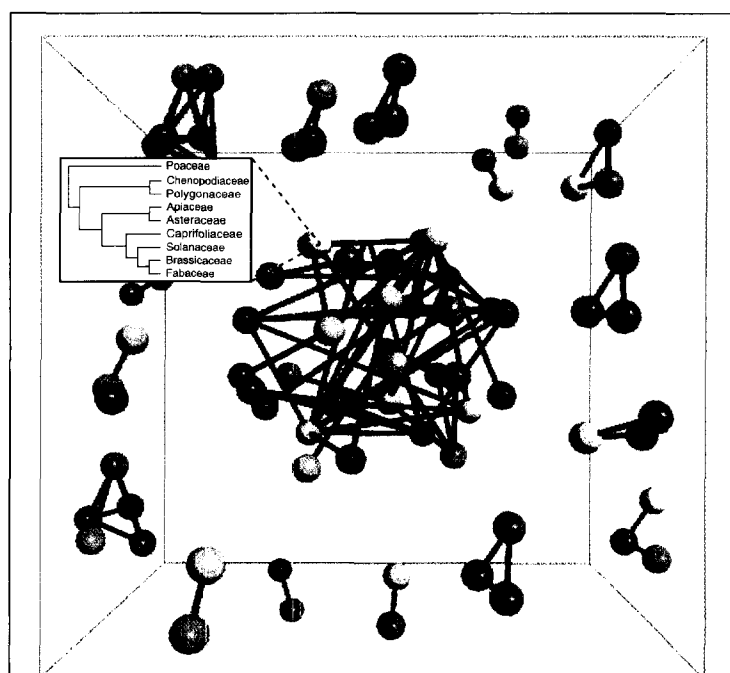
Acknowledgements

Fig. 3. Tree-graph of the phylogenies in the TreeBASE database. Each node rep-resents a phylogenetic tree found in the database; internodes connect two trees if and only if they share two or more taxa. The color of the internodes is related to how many taxa are shared between studies, with red corresponding to many and blue to only two. Yellow nodes have more taxa in their phylogenies than green nodes. Con-nected components in this graph ('islands') are candidates for supertree construc-tion. Isolated individual studies not connected to any other studies are not shown.

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