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THE (SUPER)TREE OF LIFE: Procedures, Problems, and Prospects

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■ **Abstract** Supertree construction is a new, rigorous approach for combining phylogenetic information to produce more inclusive phylogenies. It has been used to provide some of the largest, most complete phylogenies for diverse groups (e.g., mammals, flowering plants, and dinosaurs) at a variety of taxonomic levels. We critically review methods for assembling supertrees, discuss some of their more interesting mathematical properties, and describe the strengths and limitations of the supertree approach. To document the need for supertrees in biology, we identify how supertrees have already been used beyond the systematic information they provide to examine models of evolution, test rates of cladogenesis, detect patterns of trait evolution, and extend phylogenetic information to biodiversity conservation.

INTRODUCTION

The scope of phylogenetic analyses has increased tremendously over the past decade. The seed for this trend was sown by Chase et al. (1993) in an analysis of ∼500 chloroplast *rbcL* sequences sampled across angiosperms, which advanced the size of phylogenetic studies far beyond previous attempts and almost beyond the computational power then available. Now phylogenetic studies of hundreds of organisms are becoming routine (e.g., Van de Peer & de Wachter 1997, Bush et al. 1999, Soltis et al. 1999, Savolainen et al. 2000), and even those with thousands of organisms are being conducted (Källersjö et al. 1998).

Our ability to infer such large phylogenies derives from two factors. First, the molecular revolution, combined with on-line databases such as GenBank or

SwissProt, has afforded more phylogenetic data in a readily accessible format. Encouragingly, accurate answers to large phylogenetic problems may require much less data than previously thought (i.e., $<10,000$ bp) (Hillis 1996, Bininda-Emonds et al. 2000). Many studies now use sequence data on this order of magnitude (e.g., Madsen et al. 2001, Murphy et al. 2001a). Second, methodological advances are overcoming the basic limitation of phylogenetic inference, namely that the number of possible solutions to be examined ("tree space") increases super-exponentially with the number of taxa (Felsenstein 1978b). Continued advances in computer technology, in concert with algorithmic shortcuts and search strategies, will result in ever-larger phylogenetic problems becoming tractable, even if optimal solutions cannot be guaranteed (see Sanderson & Shaffer 2002, this volume).

The primary constraint to building complete phylogenies is still data accumulation. With a few notable exceptions such as the plant systematic community (e.g., Källersjö et al. 1998), data collection is largely uncoordinated and opportunistic, resulting in a patchwork of coverage for a given taxonomic group. Some species are overrepresented, whereas others are drastically underrepresented, if sampled at all. Moreover, the molecular sampling effort is confined to only a few genes, even for the more coordinated efforts. It remains unclear whether the entire extended history of a large group can be reconstructed adequately using only a few genes (but see Källersjö et al. 1998). Therefore, considerable motivation exists for developing methods that combine existing phylogenetic data—either the raw data themselves ("total evidence"; sensu Kluge 1989) or the tree topologies derived from them ("taxonomic congruence"; sensu Mickevich 1978)—to produce more inclusive phylogenies.

Recently a new approach for combining source trees—supertree construction—has gained popularity for its ability to produce phylogenies based on all data sources (i.e., morphological and molecular), even if the trees only overlap partially in the taxa they contain. Supertree construction has yielded comprehensive phylogenies for all extant members of the mammalian orders Primates (Purvis 1995a), Carnivora (Bininda-Emonds et al. 1999), Chiroptera (Jones et al. 2002b), and Lagomorpha (Stoner et al. 2003); for all extant families of mammal (Liu et al. 2001); for all species of procellariiform seabirds (Kennedy & Page 2002); for the major extant clades within the legume subfamily Papilionoideae (Wojciechowski et al. 2000); for 403 genera of the grass family Poaceae (Salamin et al. 2002); and for all genera of Dinosauria (Pisani et al. 2002).

We review the procedure of supertree construction, including its mathematical properties and potential utility to the biological community. Our discussion focuses on recent, formal supertree techniques in contrast to informal ones such as subjective syntheses of all available information (e.g., Novacek 1992) or pasting together individual hierarchically nested phylogenies (e.g., Weiblen et al. 2000) in a form of "taxonomic substitution" (sensu Wilkinson et al. 2001). Although informal methods have a long history, they lack an objective analytical methodology (Wilkinson et al. 2001); thus, our emphasis is on the more formal techniques.

DEFINITIONS AND TYPES OF SUPERTREES

Since being introduced formally by Gordon (1986), supertree construction has taken on a looser, less mathematical definition (e.g., Sanderson et al. 1998). We follow the latter to define supertree construction as the generation of one or more output trees (the supertrees) from a set of source trees that possess fully or partially overlapping sets of taxa. Because the source trees need only overlap—minimally each source tree must share at least two taxa with the rest of the set of source trees—the supertree can be more inclusive than any individual source tree contributing to it. The supertree ordinarily contains all taxa found in the set of source trees. Our definition distinguishes between supertree and consensus techniques, the latter of which we hold to combine fully overlapping source trees only (following Neumann 1983). We recognize that this distinction is arbitrary in that many consensus techniques can be adapted for a supertree setting.

Supertree techniques can be classified broadly as either "direct" or "indirect" (sensu Wilkinson et al. 2001). Direct supertree methods are akin to classical consensus techniques whereby the output tree is derived directly from source trees without a discrete intermediate step (Figure 1). Examples include strict consensus supertrees (Gordon 1986, Steel 1992), their generalization as MinCutSupertrees (Semple & Steel 2000), and Lanyon's (1993) modification of the semi-strict consensus algorithm. Informal supertrees could also be included here.

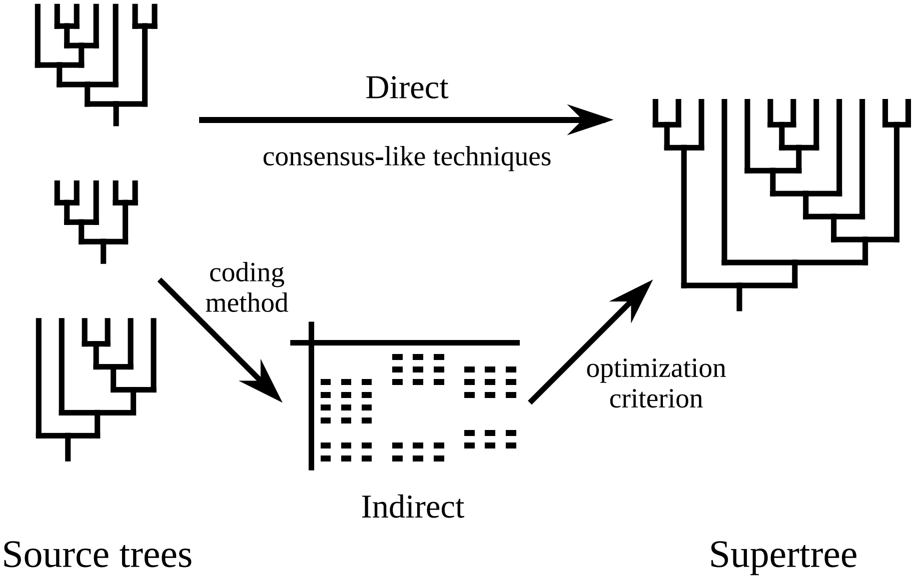
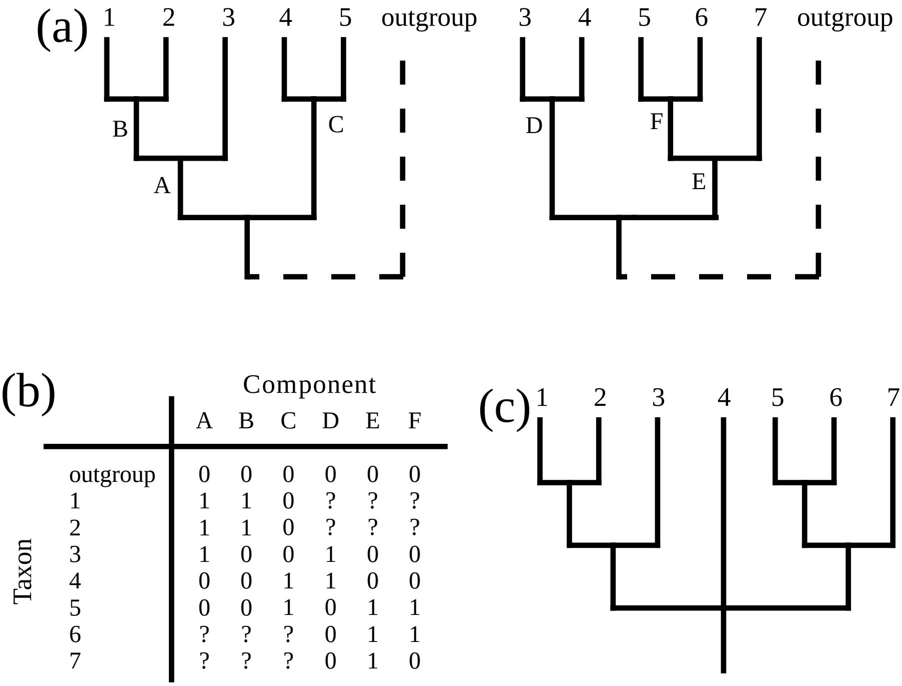


Figure 1 Diagrammatic representation of supertree construction, illustrating both direct and indirect methods.

Indirect supertree construction uses some form of matrix representation (Ponstein 1966, Ragan 1992) to encode individual source tree topologies as matrices that are then combined and analyzed using an optimization criterion (Figure 1). The best-known technique is matrix representation with parsimony (MRP) (Baum 1992, Ragan 1992; also Brooks 1981, Doyle 1992). In MRP the nodes of each source tree are encoded as follows: taxa descended from the focal node score 1; those that do not but that are present elsewhere in the source tree score 0; all other taxa are scored as missing (?). A fictitious all-zero outgroup is added to the matrix to polarize the subsequent parsimony analysis. The outgroup is then pruned to derive the supertree (Figure 2). Variants on this basic form of MRP include modifying the coding procedure (Purvis 1995b, Wilkinson et al. 2001, Semple & Steel 2002); transforming individual cells in the matrix to remove homoplasy ("flip" supertrees) (Chen et al. 2001); or using irreversible parsimony (Bininda-Emonds & Bryant 1998) or compatibility (Rodrigo 1993) to analyze the matrix. Another indirect technique is the average consensus procedure (Lapointe & Cucumel 1997). This method encodes the topology and branch lengths of source trees in individual path-length matrices, computes the average of these matrices,



Taxon	Component					
	A	B	C	D	E	F
outgroup	0	0	0	0	0	0
1	1	1	0	?	?	?
2	1	1	0	?	?	?
3	1	0	0	1	0	0
4	0	0	1	1	0	0
5	0	0	1	0	1	1
6	?	?	?	0	1	1
7	?	?	?	0	1	0

Figure 2 Matrix representation with parsimony (MRP) supertree construction. (*a*) Two source trees for the taxa 1 to 7. A hypothetical outgroup has been added to each source tree. (*b*) The matrix representations of the source trees. (*c*) The MRP supertree.

and then applies a least-squares algorithm to the average matrix to obtain the supertree.

THE THEORY OF SUPERTREES: MATHEMATICAL AND COMPUTATIONAL ASPECTS

In this section we look at some of the theory that underlies the supertree approach. In particular, we describe how concepts from discrete mathematics and computer science can illuminate three aspects of the supertree problem. First, mathematics helps formalize otherwise vague concepts (e.g., what does it mean to say that trees “fit together” consistently or that one tree “contains” another). Only once these ideas have been defined precisely is it possible to establish clear statements (theorems) concerning the properties of different supertree methods. Second, mathematical assessment can determine the limits of current or future supertree methods (“impossibility theorems”) (see Arrow 1963). Third, computational techniques can help develop and refine algorithms to construct large-scale supertrees more efficiently.

We deal with rooted trees for two reasons. First, most biologists use rooted trees. Second, and more fundamentally, the supertree problem has no satisfactory solution with unrooted source trees. For example, no supertree method that returns a single output tree can guarantee to simultaneously (*a*) treat each species equally and (*b*) display the relationships present in the unrooted source trees whenever they can be combined without conflict (Steel et al. 2000). An earlier result by McMorris (1985) also places limitations on what can be achieved with unrooted trees. Finally, even determining whether unrooted source trees can be combined without conflict is computationally intractable, or “NP-hard” in mathematical terms (Steel 1992, Böcker et al. 2000).

Formally, two equivalent ways exist to describe a (rooted) phylogenetic tree. The more common method represents the tree visually as a collection of nodes from which three or more branches lead [often called (internal) vertices and edges, respectively, in the language of graph theory]. With rooted trees, the branches inherit a natural direction; if we orient them away from the ancestral root, they point from the past to the future. This is an example of what is often called a (directed) graph. For phylogenetic trees, branches may be either internal and connect two nodes or terminal and lead to a terminal taxon. If all nodes have exactly two outgoing branches, the tree is said to be binary.

An alternative way to describe a phylogenetic tree is simply to specify its clusters (or clades) (Figure 3). If we let X denote the entire set of species under study, a cluster is the collection of species from X that are descended from the most recent common ancestor of some pair of species from X. For example, Figure 3*b* shows the clusters associated with the phylogenetic tree in Figure 3*a*. In this example the most recent common ancestor of 1 and 3 identifies the cluster $\{1,2,3,4\}$, which corresponds to the set of species that are descended from that ancestor.

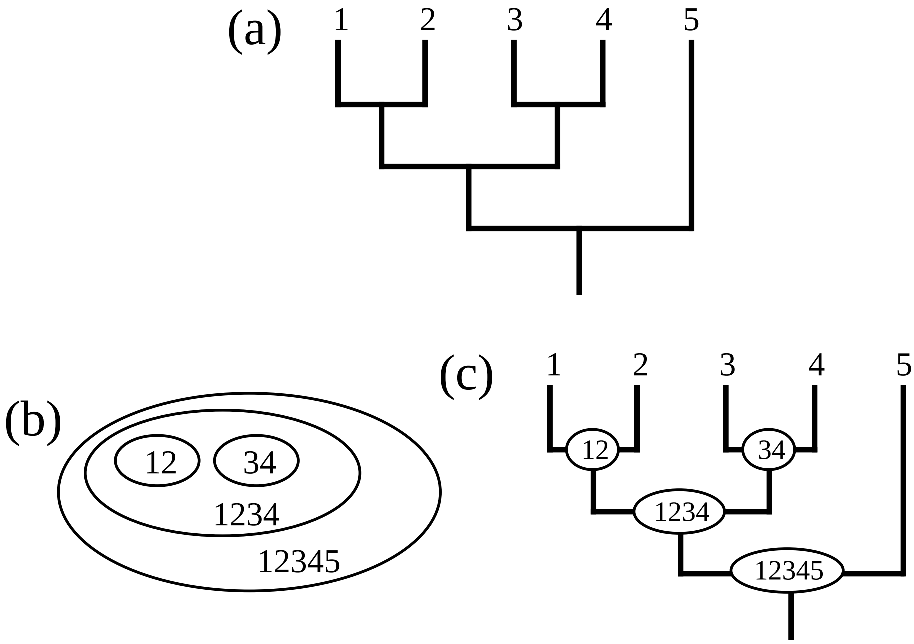


Figure 3 The equivalence between rooted phylogenetic trees and cluster systems. (*a*) A rooted phylogenetic tree *T* as a graph. (*b*) Its associated set of clusters. (*c*) The graph corresponding to this cluster system recovers *T*.

Given a collection of clusters, two fundamental questions arise that are central for many approaches to the supertree problem. Do the clusters come from a phylogenetic tree? If so, do the clusters determine this tree uniquely, and can we construct this tree easily? Regarding the first question, consider a collection *C*, composed of subsets of the entire set *X* of species. *C* forms the clusters of a phylogenetic tree for *X* precisely if all the species in *X* are contained in *C* and any two clusters *A*, *B* in *C* have the following "nesting" property: *A* and *B* either have no species in common, or all the species in one cluster are contained in the other (in set-theoretic notation, $A \cap B \in \{A, B, \phi\}$).

From such a set of the clusters, reconstructing the associated phylogeny is straightforward (Figure 3*c*). To do this, we simply place a directed branch from any cluster *A* (e.g., {1,2,3,4}) to any other cluster *B* (e.g., {1,2}) if all the species in *B* are contained in *A*, provided *A* is the smallest such cluster with this property. Thus, *A* could not be the cluster {1,2,3,4,5} in this example even though this cluster contains *B*. This process provides an equivalence between rooted phylogenetic trees and nested cluster systems that holds even when polytomies are present. Cluster representation provides the most convenient way to define certain consensus and many indirect (and informal) supertree methods.

The Ideal World: Compatible Source Trees

Consider two phylogenetic trees, T and T'. We say that T resolves T' if T' can be obtained from T by collapsing branches. In terms of clusters, this means that each of the clusters of T' is a cluster of T. Additionally, T contains T' if the phylogenetic tree that one obtains from T by deleting all taxa (and connecting branches) that do not appear in T' is equal to or resolves T'. In allowing for resolution, polytomies are held to be "soft" (Maddison 1989), reflecting uncertainty as to the exact order of speciation. Finally, a collection C of phylogenetic trees is compatible if a phylogenetic tree T exists that contains each tree in C. In this case, we call T the parent tree for the collection C. These concepts are illustrated in Figure 4. The trees in Figure 4*a* are compatible because they are contained in the parent tree in Figure 4*b*. Informally, a collection of trees is compatible if the trees tell a consistent evolutionary story and can be combined without having to suppress or alter any of the details.

For a set of compatible source trees, Gordon's (1986) strict consensus supertree method provides the strict consensus of all parent trees. Under these conditions the strict consensus and MRP supertree methods are equivalent because the MRP spectrum (i.e., the collection of all equally most parsimonious trees obtained using standard MRP) coincides exactly with the set of parent trees for the source trees. Consequently, the strict consensus MRP supertree

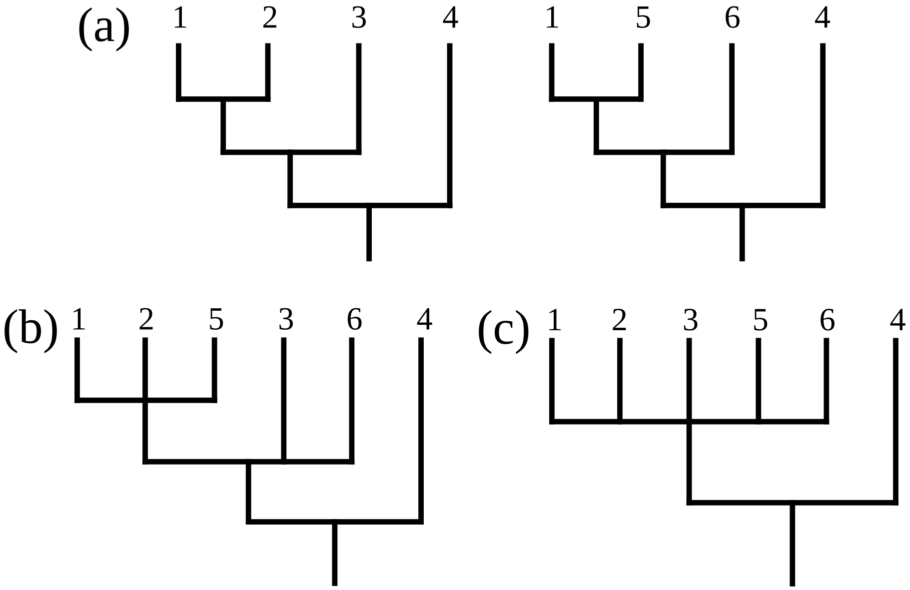


Figure 4 (*a*) Two compatible source trees. (*b*) The *BUILD* tree, which contains each of the source trees. (*c*) The matrix representation with parsimony supertree.

is identical to the strict consensus supertree of the source trees (Thorley 2000).

This finding has an important practical implication. Even for a compatible collection of source trees, computing the MRP supertree exactly may be problematic because the MRP spectrum may contain a potentially huge number of (parent) trees. However, the MRP supertree can be found quickly because it coincides with the strict consensus supertree, which can be constructed exactly by an efficient polynomial time algorithm (Steel 1992).

For compatible source trees, although each parent tree necessarily contains each of the source trees, their strict consensus (i.e., the MRP supertree or strict consensus supertree) may fail to do so. This is because there may simply be too much "slackness" in the way the source trees can fit together. For example, for the two source trees in Figure 4*a*, we may "attach" species 5 and 6 at many places within or leading to the cluster $\{1,2,3\}$ of the left source tree to obtain a parent tree. The tree in Figure 4*b* represents only one such parent tree; many more are possible, and their strict consensus is shown in Figure 4*c*. In this simple example, neither of the two source trees is contained in the MRP/strict consensus supertree.

In contrast, the *BUILD* algorithm (Aho et al. 1981) will decide whether a collection of rooted trees is compatible and, if so, construct a parent tree that contains each of the source trees. The *BUILD* algorithm builds the clusters of a tree as follows. Begin with the cluster $C = X$ (i.e., all species under study). Then repeatedly apply the following rule:

> Place an undirected branch between any two species i and j in C, provided there is some species k in C, and some source tree T for which i and j both lie in some cluster of T that does not contain k. Form new clusters by combining together species that can be connected by a sequence of branches. If this generates just one cluster consisting of all of C (and C has more than one element), then the source trees are incompatible; otherwise this step is repeated on each new cluster.

For example, again consider the two source trees in Figure 4*a*. The graph that we get for $C = X$ is shown on the left in Figure 5*a* and gives the cluster $\{1,2,3,5,6\}$ and the isolated species 4. This produces the initial tree shown on the right of Figure 5*a*. Repeating this procedure on the new cluster $C = \{1,2,3,5,6\}$ gives the graph on the left in Figure 5*b*, which produces the new cluster $\{1,2,5\}$ and the isolated species 3 and 6. This resolves the initial tree, as shown on the right of Figure 5*b*. Repeating once more for the cluster $\{1,2,5\}$ we obtain the three remaining isolated species 1, 2, and 5. Combining the three clusters obtained by this process recovers the tree shown in Figure 4*b*, which contains each of the source trees.

The *BUILD* algorithm has recently been refined. Ng & Wormald (1996) and Constantinescu & Sankoff (1995) independently showed how to output all the parent trees; Ng & Wormald also allowed hard polytomies in the source trees. As there may be many parent trees, it is useful to have an efficient algorithm that outputs just the minimally resolved parent trees (e.g., Semple 2002). Semple also

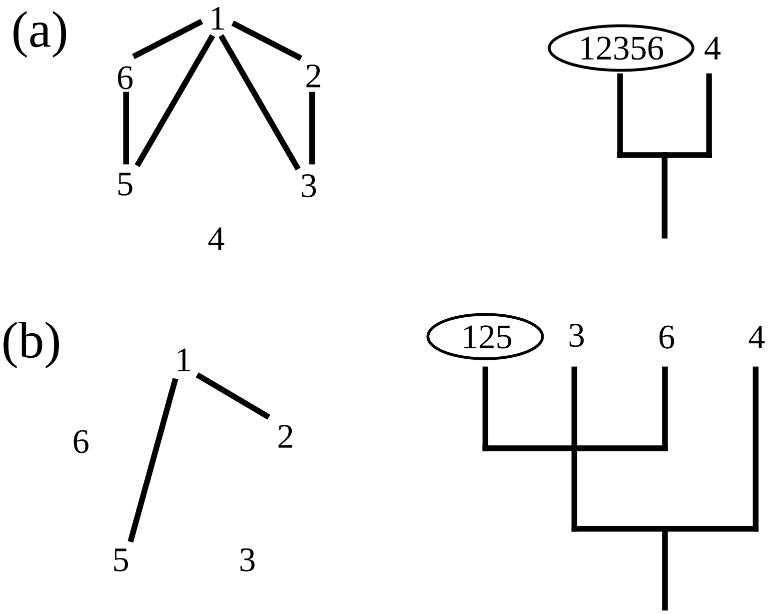


Figure 5 Diagrammatic representation of how the *BUILD* algorithm works using the source trees in Figure 4*a*. The *BUILD* supertree is given in Figure 4*b*.

characterized the *BUILD* tree in terms of a certain clustering property. It follows from this characterization that a collection of source trees has a unique parent tree if and only if the *BUILD* algorithm constructs a binary tree.

In summary, the two natural supertree approaches for compatible source trees are the *BUILD* algorithm and MRP/strict consensus supertrees. The choice of which is preferable depends, respectively, on whether the output tree should display all the source trees or only those relationships supported explicitly in the source trees. This is no longer a mathematical question; rather it represents a judgment of the biologist. For instance, it may be argued that the extra resolution the *BUILD* tree possesses over the MRP supertree in Figure 4 is misleading because neither source tree supports the cluster $\{1,2,5\}$.

The Real World: Incompatible Source Trees

In practice, some incompatibility is usually present among the source trees. Two source trees are incompatible if and only if they contain contradictory trees on the same subset of species. However, this need not be the case for three or more trees: One can easily construct examples in which every pair of trees is compatible but the entire collection is not.

Given incompatibility, two general approaches are appropriate: (*a*) try to resolve the incompatibilities by "correcting" the source trees to produce a compatible collection of source trees or (*b*) use an algorithm that does not require compatible source trees or modify an existing algorithm for this purpose.

Two strategies exist for option (*a*), both of which attempt to produce a set of compatible source trees through analyses of subtrees. The first strategy directly corrects incompatibility among trees based on quartet methods for phylogeny reconstruction (e.g., Willson 2001 and references therein). This approach has not been examined in detail but is useful in principle in a supertree framework.

The second strategy prunes "troublesome" taxa from the source trees. One approach for a small number of trees that have a considerable overlap of species is to assess if the subtrees on the species they share agree. If the reduced trees do not agree, then the source trees are incompatible. In that case, one might apply a consensus method to the subtrees and then possibly reattach the remaining species to this consensus tree (Gordon 1986, Bininda-Emonds et al. 1999). Another approach is to look for any species that show widely differing placements in the induced trees. By removing these few species, better resolution of the output tree may result (Wilkinson & Thorley 1998, Wilkinson et al. 2001), and it may be still considered a supertree because it may be more inclusive than any single source tree. However, reduced tree methods have not found wide acceptance in the biological community.

MRP is the most commonly used method under option (*b*), which we discuss in detail below. Another recent option is MinCutSupertrees, in which the *BUILD* algorithm has been adapted to handle any input of rooted trees while still preserving its desirable properties (e.g., retaining clusterings and relationships that are present in all the source trees). Essentially, whenever the *BUILD* algorithm gets "stuck" on some unbreakable cluster (see Figure 6), one deletes branches so that the cluster

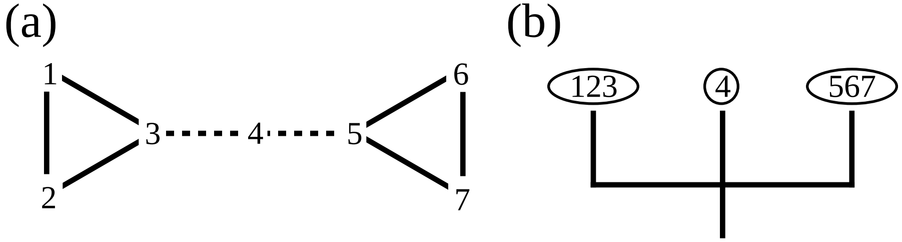


Figure 6 Unsticking the *BUILD* algorithm for incompatible source trees. Applying the *BUILD* algorithm to the source trees in Figure 2*a* (with the hypothetical outgroup taxon removed) results in the unbreakable cluster in (*a*). However, the *BUILD* algorithm can proceed if a single edge is cut, either that connecting taxa 3 and 4 or taxa 4 and 5 (*dashed lines*). Because there is no reason to cut either edge preferentially, both are cut to obtain the clusters in (*b*). Further application of the *BUILD* algorithm yields the MinCutSupertree, which in this case is identical to the matrix representation with parsimony supertree in Figure 2*c*.

breaks in a certain minimal way (for details see Semple & Steel 2000). This process can also be directed according to differential support among the source trees.

Any method of combining incompatible source trees should preserve phylogenetic relationships between species when these relationships are present in at least one source tree and are not contradicted by any other source tree. If we write $(IJ)K$ to denote the binary rooted tree in which taxa I and J form a clade to the exclusion of taxon K (the tree can also include other taxa), this desired property, $\mathbf{P_1}$, is more formally written as: If at least one source tree contains $(IJ)K$ and no source tree contains the contradictory $(IK)J$ or $(JK)I$, then the output tree contains $(IJ)K$.

However, no method can satisfy property $\mathbf{P_1}$ in general, even in the consensus setting. Consider four rooted trees for the five taxa labeled 1, 2, ..., 5 (see Figure 2 in Steel et al. 2000). Each tree has one nontrivial cluster, thereby grouping together the following pairs of taxa: $\{1,2\}$, $\{2,3\}$, $\{3,4\}$, and $\{4,5\}$. These trees contain, respectively, the subtrees (12)5, (23)5, (34)1, and (45)1; none of the source trees contains $(IK)J$ or $(JK)I$ for any subtree $(IJ)K$ in this list. Any consensus method satisfying $\mathbf{P_1}$ would have to output (12)5, (23)5, (34)1, and (45)1. However, it is obvious that no rooted phylogenetic tree can contain these four trees simultaneously.

It might be objected that the trees in this example are nonbinary. If the source trees are binary, then property $\mathbf{P_1}$ is equivalent to the (otherwise weaker) condition $\mathbf{P_2}$: if all the source trees contain $(IJ)K$ then the output tree contains $(IJ)K$. In the supertree setting, the MinCutSupertree algorithm has been shown to satisfy property $\mathbf{P_2}$ (Semple & Steel 2000). In contrast, MRP can fail to satisfy $\mathbf{P_2}$ on sufficiently contrived data, even in the consensus setting (results not shown).

A CRITICAL LOOK AT SUPERTREE CONSTRUCTION

General Criticisms

Supertree construction has been criticized strongly because, like taxonomic congruence, it loses contact with the primary data (Rodrigo 1993, 1996; Novacek 2001; Springer & de Jong 2001; Gatesy et al. 2002). Thus, Springer & de Jong have argued that supertrees present only a useful summary of the source trees, rather than an accurate phylogenetic reconstruction. Novacek added that supertrees do not provide strong tests of previous phylogenetic hypotheses because they are not based on new data sets. Slowinski & Page (1999) have also questioned how supertree analyses should be interpreted, particularly the biological meaning of any "homoplasy" (which actually only represents source tree incongruence).

However, the inherent loss of information from using the source trees is a necessary trade-off to be able to combine all possible sources of phylogenetic information. Simulation studies have demonstrated that the cost of this trade-off is not very high, at least for MRP (Bininda-Emonds & Sanderson 2001). Over a wide range of conditions, MRP performed about on a par with total evidence at reconstructing a known model tree. Also, through the use of character weighting, many supertree methods, particularly the indirect ones, can incorporate information about differential levels of evidential support both within and among source studies. The use of weighting in this manner has been demonstrated to improve the fit between the primary data and the MRP representation of their associated source tree (Ronquist 1996). Further, the simulation study of Bininda-Emonds & Sanderson (2001) showed that "weighted MRP" outperforms total evidence under most of the conditions they examined.

Another potential problem with supertree construction is data set nonindependence. For example, Springer & de Jong (2001) pointed out that the family-level mammal supertree of Liu et al. (2001) includes five different source trees that all use the same transferrin immunology data set for bats. Some nonindependence is inevitable, despite steps to minimize it (e.g., Purvis 1995a, Bininda-Emonds et al. 1999, Liu et al. 2001, Jones et al. 2002b). The effect of this problem on supertree construction is unknown. However, the interaction between the repeated data and a different suite of data sets in each source study may minimize the influence of any single repeated data set. Moreover, the different assumptions, models, and methods of analysis used mean that even source studies based on virtually the same data set can present different phylogenetic estimates. Data set nonindependence nevertheless remains a concern for supertree and taxonomic congruence approaches (unlike total evidence studies). It is likely to become more of an issue in the future as the popularity of total evidence increases and primary analyses include more and more previously published data.

Matrix Representation Techniques

Matrix representation methods have attracted the most attention in the biological community. The popularity of MRP derives both from its universal applicability (i.e., it can combine all source trees) and its ease of use. Coding of even large source trees is a trivial, if involved, process. Several programs now exist to automate this process, [e.g., PAUP* (Swofford 2002), RadCon (Thorley & Page 2000), SuperTree (Salamin et al. 2002), r8s (available from http://ginger.ucdavis.edu/r8s/)], and many parsimony programs are available for the subsequent analysis. However, in addition to occasionally failing to satisfy property $\mathbf{P_2}$ above, MRP, and by extension most matrix representation methods, have other potentially undesirable characteristics.

Although matrix representation is a well-grounded technique in basic graph and network theory, an exact one-to-one correspondence between a tree and its matrix representation exists only for single source trees (Ragan 1992). The derivation of a single supertree from an optimality analysis of the combined matrix representations must be viewed as a heuristic (Baum & Ragan 1993, Lapointe & Cucumel 1997). The behavior of matrix representation methods, and MRP in particular, is poorly characterized. MRP has a complex size bias in which the more inclusive of two competing, analogous clades is favored in the supertree because it contributes more "characters" to the matrix (Purvis 1995b, Bininda-Emonds & Bryant 1998).

MRP may also favor source trees that are more unbalanced (Wilkinson et al. 2001).

Attempts to correct for MRP's inherent size bias have been unsuccessful (Bininda-Emonds & Bryant 1998). Convex multistate coding (Semple & Steel 2002), which encodes binary source trees of any size by five multistate characters, eliminates the bias at the cost of losing the one-to-one correspondence between nodes and matrix elements. Therefore, it is difficult to incorporate information about differential signal strength within source trees using this technique.

It is debatable, however, whether MRP's size bias is problematic. If larger trees are held to be more accurate and contain more information, then the bias is appropriate (see Bininda-Emonds & Bryant 1998). More importantly, the impact of the size and balance biases appears to be minimal in practice. Simulations comparing MRP to total evidence show that both techniques produce similar phylogenies and behave similarly with respect to a number of variables (e.g., source tree size, number of source trees, and degree of taxon overlap between studies) (Bininda-Emonds & Sanderson 2001).

Direct Supertree Methods

Owing to their common usage of cluster representation, many direct supertree methods share the inability of classical consensus techniques (and, by extension, taxonomic congruence) to accommodate information regarding differential support. This is in terms of both (*a*) encoding such information within and among source studies and (*b*) summarizing such information for the supertree itself. The MinCutSupertree algorithm is uniquely able to account for differential source tree support among direct methods. It does so through a simple weighting function that dictates which of multiple possible branches to delete first to break apart a cluster (Figure 6) (Semple & Steel 2000). However, all direct methods can only provide conservative support information for the supertree. For example, the most that can be said for those clades present in a strict consensus supertree is that they are not contradicted by any source trees. At best, differential information is limited to the frequency of the clades within the set of source trees. In contrast, the clades of an indirect supertree can be characterized by various support metrics (e.g., Bremer support or bootstrap frequencies modified to account for the nonindependence within source trees). The use of such metrics for direct methods seems unlikely. Similarly, no direct method currently provides support information for the entire supertree, whereas indirect methods can through various ensemble goodness-of-fit statistics (e.g., consistency index).

APPLICATIONS OF SUPERTREES

Compared to conventional phylogenies, supertrees provide a greater potential for complete taxonomic coverage based on a consensus of all phylogenetic information (e.g., morphological, molecular, and other phenotypic traits). This feature permits broad-scale ecological and evolutionary analyses that are rarely, if ever, tractable using conventional phylogenies. Here, we review applications of supertrees (see Table 1), including novel and prospective ones. Our examples are not exhaustive and deal mainly with mammals because many supertrees are now available for them.

TABLE 1 Examples of supertrees and their applications

Supertree	Taxon	Level of tips (size)	Application	Reference[a]
Purvis (1995a)	Primates	Species (201)	Evolutionary rates	
			(Life histories)	12
			(Brain size)	6
			Extinction risk	11
			Extinction rates	10
			Immune system function	9
			Extinction and speciation	1, 5
			Brain size and behavior	2
			Allometry and home range size	8
Bininda-Emonds et al. (1999)	Carnivora	Species (271)	Evolutionary rates (Life histories)	12
			Body size and species richness	3
			Taxonomic differences	7
			Extinction risk	11
			Extinction rates	10
			Species richness	supertree study
Kirsch et al. (1997)	Marsupialia	Species (81)	Extinction and range size	4
Jones et al. (2002b)	Chiroptera	Species (925)	Extinction risk	13
Liu et al. (2001)	Mammalia	Families (90)	Phylogeny	supertree study
Weiblen et al. (2000)	Monocotyledons	Species (918)	Evolution of breeding systems	supertree study
Webb (2000)	Trees	Species (324)	Structure of ecological communities	supertree study
Linder (2000)	Restionaceae	Genera (62)	Convergent evolution	supertree study

[a] 1, Purvis et al. (1995); 2, Barton (1996); 3, Gittleman & Purvis (1998); 4, Johnson (1998); 5, Paradis (1998); 6, Deaner & Nunn (1999); 7, Bininda-Emonds & Gittleman (2000); 8, Nunn & Barton (2000); 9, Nunn et al. (2000); 10, Purvis et al. (2000a); 11, Purvis et al. (2000b); 12, Purvis et al. (2003); 13, Jones et al. (2002a).

Descriptive Systematics

Phylogenetic reconstruction involves many contentious issues (Hull 1980, Felsenstein 2001). Supertrees, if anything, have added more fuel to the fire. However, the process of culling all phylogenetic information for supertree construction is extremely useful for descriptive systematics. It helps assess what information is available, differences in relative research effort among taxa, and degree of phylogenetic congruence among studies. At the very least, supertrees highlight groups that have received little systematic attention.

For example, the MRP supertree of the higher-level relationships across eutherian (placental) mammals used 430 molecular and morphological source trees from 315 research articles (Liu et al. 2001). Taxonomic coverage was unequal among the 90 families and orders, reflecting which groups are viewed as charismatic and economically valued. Of the 1965 MRP "characters," Solenodontidae (Insectivora) was represented in only 342, whereas Bovidae (Artiodactyla) was present in 1520. Taxonomic coverage was also generally poor. In addition to bovids, only 9 other terminal taxa were represented in more than 45% of the characters. Despite this, the apparent accuracy of available phylogenies is encouraging. Except for Artiodactyla and Insectivora, which are now widely agreed to be paraphyletic, the monophyly of the remaining orders was strongly supported. Most accepted interfamilial relationships were also corroborated. The molecular and morphological trees reconstructed the same interfamilial patterns with only five exceptions, most relating to recent molecular findings involving nonmonophyly. In essence, Liu et al.'s (2001) supertree indicates that the vast majority of molecular and morphological trees are congruent for eutherian phylogeny. Any disagreement seems to stem simply from the lack of information for orders such as Insectivora and Xenarthra.

Similar patterns were found in species-level MRP supertrees of the mammalian orders Primates (Purvis 1995a), Carnivora (Bininda-Emonds et al. 1999) and Chiroptera (Jones et al. 2002b). In particular, taxonomic coverage was extremely patchy, with relationships in poorly researched groups showing less resolution in the supertree. Nevertheless, the overall resolution is high for carnivores and primates (78.1% and 79.0%, respectively, compared with a fully resolved, binary tree), reflecting both sufficient phylogenetic information to construct a supertree and generally strong agreement among the source trees. Bats reveal poorer resolution (46.4%) owing to comparatively little treatment.

When coupled with descriptive statistics, the summary of phylogenetic information assembled for supertree construction can reveal what factors influence disagreement among phylogenies. Using the carnivore supertree, Bininda-Emonds (2000) examined the effect of tree selection criteria, data source, study size, and date of study on phylogenetic reconstructions of the order. Two interesting conclusions emerged. First, widespread disparity in study effort exists. Certain groups were confirmed as receiving disproportionately more attention, discrete characters in concert with parsimony analysis were favored owing to their simplicity, and molecular trees were more abundant but covered fewer species. Second, significant differences were rare among test variables as to whether they generated differences in phylogenetic topologies. From this finding, Bininda-Emonds (2000) inferred that most estimates of carnivore phylogeny are pointing generally at the same solution.

Another way of visualizing differences between phylogenies using supertrees is through a “sliding window” form of time-series analysis in which source studies are ordered chronologically and then combined in contiguous overlapping sets (e.g., Bininda-Emonds 2000, 2003). This approach is particularly amenable to historical study, in which phylogenetic statements without an explicit data matrix characterize much of the literature. Sliding window analyses often reveal trends that are not immediately obvious. For example, the giant panda (*Ailuropoda melanoleuca*) has received tremendous systematic attention recently, partly because of its conservation importance but also because molecular analysis was held to be able to pinpoint its phylogenetic position, whereas earlier morphological studies could not (O’Brien et al. 1985). A sliding window analysis of phylogenies published from 1869 to 1999 for giant pandas and putative sister taxa showed that giant pandas are unequivocally bears and that this relationship has held prior to the advent of molecular analysis (Bininda-Emonds 2003).

Adding branch length information reflecting divergence times can enhance the descriptive utility of supertrees. Times of divergence are also of critical importance for testing macroevolutionary hypotheses (Purvis 1996, Mooers & Heard 1997; see below). Assembling fossil and molecular dates for nodes in a supertree allows analyses of the level at which independent estimates of divergence times agree. In the carnivore supertree 73 nodes had at least one date estimate from both molecular and fossil sources. In contrast to an earlier, smaller study (Wayne et al. 1991), a slight but significant difference between fossil and molecular dates was found (Bininda-Emonds et al. 1999). Additional supertrees will be valuable in verifying divergence times, measuring the tempo of macroevolutionary change, and testing whether the ages of younger or older lineages are consistently over- or underestimated between different sources of dating.

Evolutionary Models

In addition to testing rates of evolutionary change, models of evolution are inherent to applying comparative phylogenetic methods for tests of adaptation and character evolution. The commonly accepted null model of evolution is Brownian motion (Felsenstein 1985), in which the amount of character evolution scales to branch length. Under this model closely related taxa are more similar to one another than to more distantly related ones. Although this is an effective null model for various macroevolutionary tests (Purvis et al. 1994), we do not know whether it is correct. Non-Brownian motion models also exist and are theoretically viable (e.g., Price 1997, Harvey & Rambaut 2000; see also Losos 1999). This is where supertrees should come into the picture. With a complete tree and associated branch lengths, characters could be correlated with tree structure to examine how species are evolving relative to each model and whether morphological, life history, or behavioral traits are actually following non-Brownian motion models.

Rates of Cladogenesis

Despite considerable effort, at least two fundamental questions about the tempo and mode of macroevolutionary change remain. First, do different lineages show different patterns of speciation and extinction? Second, how are any differential patterns related to rates of evolution? Investigating these questions hinges on complete taxonomic coverage (Nee et al. 1992, Pybus & Harvey 2000), which supertrees can provide. Based on the primate supertree, it was shown that speciation and extinction probably do not vary through time in this group (Purvis et al. 1995, Paradis 1998), although there may be variable rates at lower taxonomic levels using some statistical criteria (Pybus & Harvey 2000). Analysis of the carnivore supertree revealed that eight lineages contain significantly more species than expected by chance if all lineages had equal probabilities of diversifying (Bininda-Emonds et al. 1999).

A future trend in supertree applications will be comparing patterns and processes among trees. For example, whereas primates have had few explosive radiations for certain isolated clades only, carnivores have had massive radiations occurring many times among independent clades (Purvis et al. 1995, Bininda-Emonds et al. 1999). Analogous analyses on an informal supertree of flowering plants show that 10 clades are unexpectedly rich in species, whereas 13 clades have a lower than expected number (Magallón & Sanderson 2001). The distribution of these clades indicates that specific characteristics are unlikely to have promoted diversification within angiosperms. These patterns not only raise interesting questions about what factors lead to high diversification rates in some taxa, but also pertain to important consequences for conserving future biodiversity (see “Biodiversity and Conservation” below).

With an incomplete phylogeny, it is difficult to test for differential patterns of species richness (Pybus & Harvey 2000). The completeness of supertrees thus allows us to test null models of diversification (see Simberloff et al. 1981, Purvis et al. 1995). Even without knowing actual speciation and extinction parameters, simulation can be used to find the richness patterns generated using different values, which can be compared against the supertree. For example, such a simulation analysis compared against the carnivore supertree revealed that a massive extinction event likely occurred within the past five million years that killed off two thirds to five sixths of all species (Purvis et al. 2001). Even though these numbers are rough approximations, they are not the result of perceived losses from species not included in the tree.

Evolutionary Patterns

The surprisingly modern realization that hierarchical relationships among taxa are represented by phylogenies revolutionized comparative evolutionary biology (Felsenstein 1985, Harvey & Pagel 1991). The resultant interest in simply diagnosing the macroevolutionary patterns between traits and trees (Gittleman & Kot 1990, Martins 1996, Losos 1999) was limited by a lack of comprehensive phylogenies. Initially, researchers turned to taxonomies, which are often poor reflections of phylogenies. Supertrees, owing to their increased completeness, allow us to address questions of a broader scope with increased power. They also mitigate the known adverse effects in comparative analyses associated with incomplete taxon sampling (see Gittleman 1989).

The use of a supertree allows proper tests of functional relationships. For example, using the primate supertree with an independent contrasts analysis, Nunn & Barton (2000) found that home-range size scales to body mass with an exponent of 0.75 following Kleiber's law, not 1.0 as suggested by other comparative studies. Similar comparative studies have benefited from using supertrees to investigate brain size evolution in primates (Barton 1996), convergent evolution in vascular plants (Linder 2000), abundance patterns in Australian marsupials (Johnson 1998), and immune system functions in primates (Nunn et al. 2000). All these studies required supertrees because of their scope; without supertrees, sample sizes would often have been halved.

Comparative tests to associate differences in species richness with changes in a given trait likewise require complete phylogenetic information. For example, frequency distributions of body sizes in a clade are generally right-skewed. Most species tend to be small-bodied, perhaps because small-bodied lineages have the biological properties to speciate at higher rates. Previous attempts to test this hypothesis have been hampered by missing taxa, inadequate comparative statistics, and no null model for comparisons. Using the carnivore and primate supertrees, Gittleman & Purvis (1998) showed for the first time that species richness is not related to body size in primates and only partially so in carnivores, appearing mainly in the "dog-like" carnivores (i.e., canids, procyonids, pinnipeds, ursids, and mustelids).

Finally, supertrees have been used to test the "evolutionary lag" phenomenon (see Harvey & Pagel 1991), an oft-cited reason for failing to find macroevolutionary patterns among traits that are expected to be related. For example, observed slopes of brain size on body size in mammals are usually less than isometric, with taxon-level effects revealing shallower slopes at higher taxonomic levels. This is consistent with evolutionary lag in brain size evolution (Lande 1979, Pagel & Harvey 1988). Although this explanation is prevalent in the literature, inadequate samples across independent clades prevented direct tests of it. Deaner & Nunn (1999), using the primate supertree together with a method they developed to measure the relative change in two traits along the same time axis (branch), found no evidence for evolutionary lag in brain size. Because the method can only be used on sister species, supertrees are essential; sample sizes would otherwise be prohibitively small. In this example, only 22–25 contrasts were available across the order, even with the complete supertree.

Biodiversity and Conservation

Although appreciated for some time (Vane-Wright et al. 1991; see Vázquez & Gittleman 1998 for additional references), the importance of phylogenies to conservation was highlighted by Nee & May (1997). Using simulation and analytical modeling, they showed that evolutionary history need not necessarily be lost at a profound rate if (*a*) extinction is random, (*b*) branch lengths are used to represent a measure of "phylogenetic diversity" (PD), and (*c*) the topology of the tree is relatively balanced. The realism of these simulations could be tested using supertrees. For instance, Purvis et al. (2000a) used the primate and carnivore supertrees to compare the amount of PD lost if species classified as threatened went extinct relative to random extinction. Greater amounts of PD would indeed be lost. Interestingly, only the primates showed a significant loss. This is consistent with expectation (Nee & May 1997, Heard & Mooers 2000): The primate supertree is more unbalanced than the carnivore supertree (compare Purvis 1995a, Bininda-Emonds et al. 1999), revealing the underlying effects of random extinction. If incomplete trees were used for these groups, it would not be possible to separate the effects of extinction models relative to phylogenetic incompleteness. Similarly, Sechrest et al. (2002) used the carnivore and primate supertrees to show that PD is not randomly distributed, in that the 25 designated global biodiversity hotspots harbor significant amounts of PD.

Supertrees have also helped in investigations of the factors that may contribute to extinction risk. Despite many reviews of these factors (see McKinney 1997), empirical tests have been lacking because of too few comparative databases and comprehensive phylogenetic estimates. Purvis et al. (2000b) assembled trait data on carnivores and primates and performed contrast analyses using the supertrees of each group. Of 12 possible variables, high trophic level, low population density, slow life history (particularly gestation length), and especially small geographic range were significantly and independently correlated with the International Union for Conservation of Nature and Natural Resources (IUCN) *Red List* extinction risk designations. The traits combined explained nearly 50% of the variation across species. Supertrees were again essential. Without them, a multivariate analysis would not have been possible. Even with the complete supertrees, slightly less than 50% of all species were represented in the complete multivariate model. In the face of not having complete molecular or morphological phylogenies in the near future, supertrees are important tools for contributing information about the biological past in order to conserve present and future evolutionary history.

CONCLUSION: THE FUTURE OF SUPERTREE CONSTRUCTION

An unspoken sentiment is that supertree construction merely represents a stopgap measure, possibly based on economic grounds (see Sanderson et al. 1998), to infer the tree of life until there is sufficient molecular data. However, there are three strong arguments against this viewpoint.

The first relates to sampling issues. Despite the tremendous increase in sequencing effort, most species will continue to be poorly characterized at the molecular level for the foreseeable future. For example, two recent large-scale molecular studies across mammals (Madsen et al. 2001, Murphy et al. 2001a) together sequenced only 146 species, 27 of which were in common; a combined and expanded third study by both groups increased the number of common species sampled to 42 (Murphy et al. 2001b). Although prodigious, this represents a fraction of the approximately 4500 extant species of mammal, which in turn represent a fraction of the earth's total biota, much of which is not studied as intensively. Future sampling effort will continue to be nonrandom, with priority being given to species that are of economic or conservation importance, or that are simply more appealing to us (O'Brien et al. 2001). Thus, phylogenetic inference of molecular data will be prone to problems from taxon sampling (Lecointre et al. 1993, Bininda-Emonds et al. 1998, Hillis 1998), long-branch attraction (Felsenstein 1978a, Huelsenbeck 1995), and missing data (Sanderson et al. 1998, Wiens 1998).

The second argument arises from analytical problems inherent to molecular data, particularly in a maximum likelihood framework. Especially for noncoding DNA, assessing homology and therefore aligning the sequences becomes more difficult as the included taxa become increasingly diverse (Sanderson et al. 1998). There is also the computational demand of incorporating appropriate models of molecular evolution, models that are becoming increasingly sophisticated and complex (Sanderson & Shaffer 2002, this volume). Different genes are often analyzed most appropriately using different evolutionary models. However, current computer programs are limited in their ability to incorporate multiple models. The computational demand of such analyses is probably prohibitive in the foreseeable future (Sanderson & Kim 2000), necessitating the use of overly simplistic analyses (e.g., Gatesy et al. 2002). Instead, it seems more efficient to analyze each gene separately under an appropriate evolutionary model and then combine the results as a supertree (see Doyle 1992).

Finally, there is the need to include nonmolecular data. The inclusion of fossil taxa, for which molecular data are normally unavailable, can overturn phylogenetic hypotheses based on extant species (Donoghue et al. 1989). Moreover, the principle of total evidence dictates that the best hypothesis is that derived from as many independent data sources as possible. The nonindependence of molecular data owing to linkage associations between genes is often underestimated. For example, it is often argued that mitochondrial DNA with its many genes constitutes a single phylogenetic data source because it forms a single heritable unit that is not normally subject to recombination (Cummings et al. 1995). Although extremely valuable, molecular data represent only one tool to reconstruct the tree of life.

In summary, we maintain that supertree construction has a valid and continuing role in phylogenetic systematics. Although simultaneous analysis of the primary data is preferable owing to the greater information content retained, its applicability is limited by incompatible data types and the requirement of a single optimization criterion. Current supertree methods are not perfect. However, they generally show good performance in simulation, suggesting that we can be reasonably confident in the phylogenetic estimates derived from them. Supertree techniques continue to be developed, and advances such as MinCutSupertrees and flip supertrees are likely to improve the performance of supertree construction in the future.

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