

Chapter 20

SUPERTREES

Using complete phylogenies in comparative biology

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Abstract: The field of comparative biology has undergone a renaissance since researchers began examining macroevolutionary questions in an explicit phylogenetic framework. However, research into these new areas is now hampered by incomplete phylogenetic information for the clades of interest. Species-level trees made by supertree construction techniques offer a way to generate complete phylogenies. Here we review the types of questions that can now be addressed and evaluate critically when using complete trees made by supertree construction techniques might be inappropriate.

Keywords: biodiversity; comparative methods; conservation; extinction; phylogenies; speciation; trait evolution

1. Introduction

Since Darwin (1859), the comparative method has been used to ask questions about patterns of evolutionary change. It has long been recognized that there are two components affecting patterns of evolutionary change: that of adaptation to environments and of lineage-specific effects that are invariant with the environment (Darwin's "conditions of existence" and "unity of type", respectively). However, only recently have more formalized techniques been developed to measure the relative contributions of these two components by incorporating the pattern of evolutionary change directly into comparative analyses, thereby leading to a re-invigoration of this field (Harvey and Pagel, 1991). Application of these comparative phylogenetic techniques have led to key insights into a diverse array of important biological questions over the past decade, including patterns of correlated

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trait evolution (e.g., evidence for the mosaic evolution of the mammalian brain; Barton and Harvey, 2000) and patterns of co-speciation (e.g., co-evolution of pocket gophers and their parasitic lice; Morand *et al.*, 2000). Complete phylogenies are necessary for answering questions about the evolutionary process itself — speciation and extinction — and for controlling lineage-specific effects when studying patterns of adaptation.

Unfortunately, complete trees are difficult to generate. Molecular sampling in different clades is often opportunistic, leading to poor clade coverage. Sampling for morphological traits is usually more complete, but trees generated by these data are often less formal analytically and of poor resolution (e.g., taxonomies). Supertree construction techniques offer exciting new opportunities to examine the nature of evolutionary processes because they can generate complete phylogenies of entire large clades quickly based on multiple lines of evidence (Bininda-Emonds *et al.*, 2002). Additionally, supertrees introduce less error as a result of taxon sampling artifacts, and therefore provide a means for truly examining macrobiological patterns across complete clades. In this chapter, we consider what kind of evolutionary questions one can ask uniquely with complete phylogenies and the possible future applications of such phylogenies. Additionally, we evaluate critically when using complete trees made by supertree construction is inappropriate to examine these new questions. We focus here on comparative evolutionary applications for complete supertrees rather than for trees in general because the latter is covered elsewhere (e.g., Harvey and Pagel, 1991).

2. Descriptive systematics and priority setting

Most of our discussion here deals with unique uses of supertrees for comparative hypothesis testing because supertrees allow us to gain access to comprehensive and large phylogenies. At the outset, therefore, we want to discuss briefly how supertrees can be used to diagnose whether taxonomic completeness is possible. Complete phylogenies made by supertree construction techniques are an extremely valuable tool in descriptive systematics. In the process of culling the phylogenetic information for all species within a clade from published phylogenies, differences in systematic effort among taxa can be quantified, thereby identifying groups that are desperately in need of more research and providing a starting point for future studies. For example, a recent supertree study of Chiroptera (bats) revealed that over one-third of all phylogenetic studies have investigated one family (Phyllostomidae), although it represents only one-sixth of all bat species (Jones *et al.*, 2002). At the other extreme, several bat clades have never been

Table 1. Phylogenetic resolution and sampling effort in different bat clades (OW = Old World, NW = New World). For each clade, N_{taxa} = number of taxa; $\%_{\text{RES}}$ = resolution of the supertree topology as a percentage of a fully bifurcating solution; N_{sour} = number of independent source trees; and N_{char} = number of binary characters recoded from the source tree topologies into the supertree matrix (Jones *et al.*, 2002). Poor resolution results from both poor coverage per species ($N_{\text{char}} / N_{\text{taxa}}$) and poor sampling in each study ($N_{\text{char}} / N_{\text{sour}} / N_{\text{taxa}}$) for Kerivoulinae and Rhinolophidae. However, low resolution in Megadermatidae, Hipposideridae and Pteropodidae is more likely a result of disagreements between source trees as the coverage per species and sampling level for each clade is relatively high.

Clade	N_{taxa}	$\%_{\text{RES}}$	N_{sour}	N_{char}	$N_{\text{char}} / N_{\text{taxa}}$	$N_{\text{char}} / N_{\text{sour}} / N_{\text{taxa}}$
Kerivoulinae (Wooly bats)	22	10.0	2	4	0.18	0.09
Rhinolophidae (Horseshoe bats)	64	17.7	5	58	0.91	0.18
Megadermatidae (False vampire bats)	5	33.3	4	8	1.60	0.40
Vespertilioninae (Vesper bats)	268	35.6	32	321	1.20	0.04
Murininae (Tube-nosed bats)	16	35.7	2	8	0.50	0.25
Hipposideridae (OW leaf-nosed bats)	66	35.9	6	85	1.29	0.21
Pteropodidae (OW fruit bats)	166	46.1	14	265	1.60	0.11
Miniopterinae (Long-fingered bats)	10	50.0	2	5	0.50	0.25
Molossidae (Free-tailed bats)	80	56.4	12	125	1.56	0.13
Nycteridae (Slit-faced bats)	12	60.0	3	14	1.17	0.39
Phyllostomidae (NW leaf-nosed bats)	141	66.2	39	630	4.47	0.11
Natalidae (Funnel-eared bats)	5	66.7	2	4	0.80	0.40
Emballonuridae (Sheath-tailed bats)	47	68.9	11	113	2.40	0.22
Mormoopidae (Naked-backed bats)	8	83.3	7	23	2.88	0.41

investigated cladistically (Kerivoulinae, Miniopterinae, Murininae, Natalidae, and Rhinopomatidae; Table 1), and should be a natural focus for future research. The disproportionate information available for certain taxa seems a function of which groups are viewed as charismatic and economically valued, and little to do with their importance to the diversity of the clade. For example, a supertree study of all eutherian (placental)

mammals found only ten clades that were represented in more than 45% of the total information that was used to construct the supertree: Bovidae (cows), Balaenopteridae and Delphinidae (whales and dolphins), Carnivora (dogs and cats), Caviidae and Muridae (cavies and rats), Equidae (horses), Leporidae (rabbits and hares), Primates, and Suidae (pigs) (Liu *et al.*, 2001). The analyses implemented when building supertrees are useful in identifying such trends.

The relative support for relationships of taxa within different clades can also be quantified using this approach and used to set priorities for future research by distinguishing between those relationships that are poorly resolved because they are less studied or because of disagreement among the source trees (Table 1). Complete trees based on supertree techniques can also be used to assess differences among phylogenies for a given group through a “sliding window” time-series analysis that shows how species have fit into published phylogenies over time. For example, such an analysis from supertree data collection of phylogenies from 1869 to 1999 showed that the giant panda was always held unequivocally to be more closely related to bears than to raccoons, even before the advent of molecular analysis (Bininda-Emonds, in press).

3. Trait co-evolution

Traditionally, comparative biology was interested in how traits co-evolve with one other. For example, for the relationship between diet and brain size in primates, it has been shown that fruit-eating species have larger neocortex sizes relative to the size of the rest of their brains (Barton, 1998). However, it was recognized that such comparisons might violate statistical assumptions when the methods assume that data points are independent of one other (Felsenstein, 1985; Harvey and Pagel, 1991). Because species are related through evolutionary descent, they often inherit similar traits; therefore, it is unlikely that the trait values of species are independent statistically (although not impossible under different trait evolutionary models; Losos, 2000; Martins *et al.*, 2002; see below). Phylogeny is now incorporated routinely in comparative biology to control for this statistical non-independence. The use of complete phylogenies has helped expand the scope of the questions that can be addressed across diverse, independent clades: for example, in studies of convergent evolution in vascular plants (Linder, 2000), abundance patterns in Australian marsupials (Johnson, 1998), immune system functions in primates and carnivores (Nunn *et al.*, 2000, 2003), and correlates of extinction risk in primates, carnivores, and bats (Purvis *et al.*, 2000b; Jones *et al.*, 2003). Additionally, questions about the rate and nature of trait change

Table 2. Phylogenetic signal in life history and ecology traits in mammals. N = sample size, λ = the maximum likelihood estimate of the phylogenetic signal parameter for each trait (values of 0 indicate traits have no phylogenetic component, whereas values of 1 indicate that the trait is correlated perfectly with phylogeny), $\ln \text{lik}$ = log likelihood of the model when $\lambda = 0$ and significance of values of λ being greater than 0. ** $p < 0.01$, *** $p < 0.001$ (adapted from Freckleton *et al.*, 2002).

Trait	N	λ	$\ln \text{lik}, \lambda = 0$
Body mass	60	1.00	-161.31 ***
Diet	60	1.00	-95.21 ***
Latitude	60	0.67	-230.68 **
Home range size	43	0.00	-91.25
Metabolic rate	26	1.00	-54.17 ***
Lifespan	26	1.00	-27.25 ***

across the phylogeny can now be examined more comprehensively by using complete phylogenies that have some measure of divergence in units of time (branch lengths). Dating techniques are in their infancy for complete trees where not all taxa have some measure of sequence divergence (Purvis, 1995; Bininda-Emonds *et al.*, 1999), but are improving rapidly (Sanderson, 2003; Bryant, 2004; Vos and Mooers, 2004; Jones *et al.*, in prep.). Here, we review three areas where complete and large supertrees will improve analyses of trait co-evolution: quantifying phylogenetic signal in traits, examining models of trait evolution, and identifying sister taxa to generate statistically matched pairs.

3.1 Phylogenetic signal in comparative biology

Recent interest has focused on quantifying how much traits are influenced by phylogeny or contain “phylogenetic signal” (Freckleton *et al.*, 2002; Blomberg *et al.*, 2003; see Table 2). It has become important to quantify how much phylogenetic signal each trait shows because the newer, more powerful phylogenetic comparative methods control for the exact amount of phylogenetic signal in each trait when investigating trait co-evolution (e.g., Pagel, 1999; Blomberg *et al.*, 2003). There are now several different methods of estimating the amount of phylogenetic signal in traits (e.g., Cheverud *et al.*, 1985; Gittleman and Kot, 1990; Abouheif, 1999; Pagel, 1999; Blomberg *et al.*, 2003). These tests are dependent on the clade size and the accuracy of the tree topology and trait data (Bininda-Emonds and Gittleman, 2000; Blomberg *et al.*, 2003). Using complete phylogenetic information about the clade can improve the accuracy of both the topology (see Hillis, 1996) by reducing the effects of long-branch attraction and the

measure of phylogenetic signal in the traits by increasing the number of taxa in each clade that can be considered.

3.2 Models of trait evolution

By using more complete, large supertrees, it is also possible to test models of how different traits have evolved. In most phylogenetic comparative methods, models of trait change are assumed in which closely related species have traits that are more similar than those between more distantly related ones (Felsenstein, 1985). Two common models assume that trait change is directly proportional to either elapsed time or to the number of observed speciation events (referred to typically as the “Brownian motion” and “punctuational” models, respectively; see Harvey and Pagel, 1991; Purvis *et al.*, 1994). However, the accuracy of these models is unknown empirically, although each is an effective null model for various phylogenetic comparative tests (Purvis *et al.*, 1994) and hundreds of comparative papers hinge on them. Using other models of trait evolution, of which there are many (see Harvey and Rambaut, 2000), closely related taxa can have traits that are more different than between distantly related taxa such that the amount of trait evolution does not scale to the phylogeny (Price, 1997; Losos, 2000; Martins *et al.*, 2002). With complete supertrees that include divergence times, characters can be examined across the tree to examine how traits are changing relative to what would be expected from each model. Simulation studies indicate clearly that these non-Brownian-motion models are viable theoretically (Harvey and Rambaut, 2000), and complete trees can tell us which traits follow which models, with revisions of comparative statistical methods to follow suit.

3.3 Sister taxa comparisons

In comparative biology, comparing sister taxa is an extremely powerful tool to examine patterns of trait evolution. Sister taxa are the same age (they diverged at the same time from a common ancestor) and share many traits, and so form a statistically matched pair. Complete trees are crucial to identify sister taxa because the identified closest related taxon could be incorrect if the phylogenetic information is incomplete (Figure 1). Using complete phylogenies enables accurate identification of matched pairs on which to test hypotheses, and this is particularly important when the question relies on an estimate of time since divergence of these two taxa. We review briefly three areas of research that rely typically on comparisons across sister taxa and would benefit particularly from complete phylogenies.

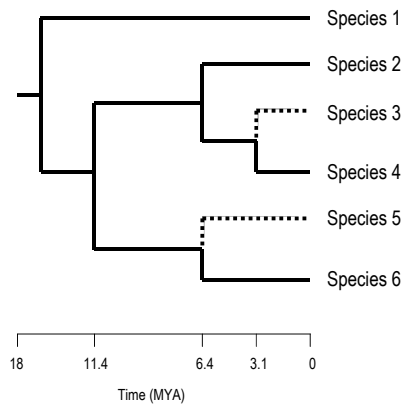


Figure 1. Estimating sister taxa and divergence times. Missing taxa (dashed lines) can cause sister taxa to be estimated incorrectly (e.g., species 2 would be considered wrongly to be the sister taxon of species 4) and divergence times to be overestimated (e.g., divergence time for species 4 from its most recent common ancestor would be calculated as 6.4 million years, not 3.1).

3.3.1 Age and area models

Interest in geographic range evolution has focused historically on how range size changes over the evolutionary lifespan of a taxon: at speciation, a new species inherits a proportion of the range of its ancestor and, at extinction, range size declines to zero. Several models of range-size change have been proposed (see Gaston, 1998; Jones *et al.*, in press for reviews), but diagnosis of these models requires that the range of a species is known throughout its evolutionary history. An alternative approach is to examine interspecific variation in range sizes of contemporary species as representative of an intraspecific trend (e.g., Webb and Gaston, 2000). Here, phylogenetic age (the age at which a species diverged from its sister taxa; see Figure 1) is correlated against current range size. Measuring phylogenetic age in this manner requires that the phylogenetic information for all the taxa in the clade of interest is known. Missing taxa would overestimate the phylogenetic age of all species in the phylogeny (extinct taxa could also have the same effect, although obviously this is more difficult to account for). Using complete trees is crucial to estimate phylogenetic age correctly and to investigate these questions.

3.3.2 Speciation models

Sister-pair comparisons have been used to identify the spatial mode of speciation in different clades by investigating the overlap of their geographic

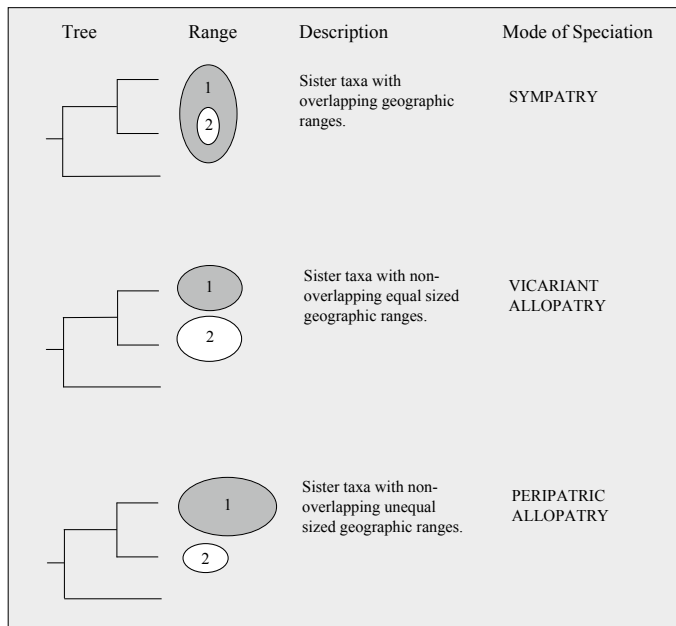


Figure 2. Models of speciation. Current geographic distributions of sister taxa (species 1 and 2) can be used to infer modes of speciation (adapted from Losos and Glor, 2003).

range distributions (Figure 2). With complete trees, the pattern of geographic ranges can be examined with reference to the entire phylogeny (Barracough *et al.*, 1998; Barracough and Nee, 2001; Losos and Glor, 2003). The degree of sympatry (overlap) in geographic ranges of sister taxa can be estimated and plotted against their time since divergence. The mode of speciation (e.g., allopatric or sympatric) can be determined from the deviations from a null model (e.g., geographic range shifts are stochastic following speciation events). Clearly, if the phylogeny is incomplete (or there are “hidden extinctions”), then the estimated degree of overlap and time since divergence between sister taxa can be wrong. Many studies suggest that an allopatric pattern is the most common mode of speciation (e.g., in primates, fruit flies, and North American tiger beetles; Barracough *et al.*, 1998). It is hoped that further analyses with more complete species-level trees will test the generality of these patterns in a broader range of taxa. As Losos and Glor (2003) point out, the assumptions that these methods make (e.g., assuming that current ranges reflect the distribution of species at speciation) need to be tested more rigorously before these results are convincing.

The correlation between phenotypic disparity and the mode of speciation can also be examined using sister-pair comparisons. For example, there

might be a positive relationship between phenotypic dissimilarity and degree of sympatry if phenotypic differences are necessary for sympatric species to co-exist. Alternatively, there might be a negative relationship if phenotypic variation evolves as a consequence of geographical variation in environmental conditions. There is some evidence that different patterns operate in similar clades (e.g., tiger beetles; Barraclough *et al.*, 1998; Barraclough and Vogler, 2000), and further tests are needed across more complete phylogenies.

3.3.3 Trait evolutionary lags

One of the most common reasons given for failure to find significant correlation among traits is the “evolutionary lag” phenomenon (see Harvey and Pagel, 1991). A well-cited example of this phenomenon is for brain:body size allometry in mammals. Observed slopes of brain size on body size are very often less than isometric, with taxonomic differences revealing shallower slopes at higher levels, suggesting evolutionary lag of brain size not responding to selection as quickly as body size (Lande, 1979; Pagel and Harvey, 1988). Deaner and Nunn (1999) developed a method for measuring relative change of one quantitative trait compared with another (e.g., brain versus body size) along the branches of a phylogeny without assuming any explicit model of evolution (but requiring meaningful branch lengths). As one trait changes along a branch, it is measured relative to the other trait changing along the same branch; comparisons are then made for all sister taxa. Using this method on the complete species-level primate supertree (Purvis, 1995), no evidence was found for evolutionary lag in brain size. As with all analyses that rely on phylogenetic age, it is crucial that all taxa in the clade are present; otherwise, an observed pattern might result from missing taxa rather than being a true pattern resulting from all trait values. With complete sampling, the approach can be used to examine the rate of evolution of different traits more widely (e.g., Purvis *et al.*, 2003; see also Moore *et al.*, 2004). Without a supertree, it would not be possible to examine rate change between traits because a phylogeny must be fairly large and comprehensive, characteristics that are rare even for well-studied groups.

4. Patterns and processes of cladogenesis

Considerable attention in comparative biology is now turning to patterns and processes of cladogenesis (Allen *et al.*, 2002). A glance at almost every phylogeny reveals that some clades have more species than others. However,

to examine clade-richness meaningfully, comparisons of clade size need to be made between clades of the same age (Barracough *et al.*, 1998). This can be done by comparing the sizes of sister clades (by definition the same age) and / or by estimating divergence times across the entire tree to determine rates of cladogenesis. For either analysis, complete trees for the clade of interest are crucial (Barracough *et al.*, 1998), and provide us with an exciting opportunity to test hypotheses about the evolutionary process itself. Here, we discuss developments in two current areas: 1) whether rates of cladogenesis differ between clades and 2) identifying biological or ecological correlates of different cladogenesis rates.

4.1 Rates of cladogenesis

Investigation into rates of cladogenesis relies either on the topology of the tree to compare diversification rates of sister clades (e.g., Slowinski and Guyer, 1989; Kirkpatrick and Slatkin, 1993; Moore *et al.*, 2004) or on the branch lengths (nodal dates) of the tree (e.g., Nee *et al.*, 1992, 1994) to estimate rates of cladogenesis. For methods that rely on the topology alone, a complete tree is necessary so that sister-taxa can be chosen accurately. Additionally, to obtain a measure of tree balance (Kirkpatrick and Slatkin, 1993), it is imperative to have all the species within a clade represented; otherwise, the comparisons between the number of taxa in each clade will be affected by taxon sampling. For the methods that use nodal dates within birth-death or coalescent processes to estimate rates of cladogenesis (e.g., Nee *et al.*, 1992, 1994), a complete phylogeny is not required. Methods have been developed to take missing taxa into account on trees built from molecular sequences (Pybus and Harvey, 2000; Pybus *et al.*, 2002). However, if a molecular tree is not available, it is important to have a complete tree to allow accurate calculation of branch lengths (see Section 7.1). Both topology and branch-length based methods have been used in conjunction with supertrees to look at evolutionary processes. For example, a constant rates birth-death null model (Nee *et al.*, 1992, 1994) was used to identify clades that contain more species than expected in the complete species-level supertree of the primates (Purvis, 1995). Cercopithecidae (Old World monkeys) were found to have a higher diversification rate than other primate lineages (Purvis *et al.*, 1995), a result that was found later to hold irrespective of null model used (Paradis, 1998; see also Moore *et al.*, 2004).

4.2 Correlates of cladogenesis

A complete phylogeny coupled with trait databases can be used to investigate correlates of cladogenesis or “key innovations”. Several

biological and ecological traits have been shown to cause lineages to become more diverse: phytophagy in insects (Mitter *et al.*, 1988), sexual dichromatism in birds (Barraclough *et al.*, 1995; Owens *et al.*, 1999), and polyandry in insects (Arnqvist *et al.*, 2000) are some examples (but for a counterexample of sexual selection and speciation rate in birds, see Morrow *et al.*, 2003). Until recently, rigorous hypothesis testing was limited to discrete characters compared across sister clades (reviewed in Barraclough *et al.*, 1998). However, the types of questions that can be addressed have exploded with the development of statistical methods for analyzing continuous character states simultaneously in a nested hierarchy of phylogenetically independent comparisons (Isaac *et al.*, 2003). The effect of continuous characters such as body size, sexual dimorphism, and group size and composition on species-richness now can be addressed rigorously, but only in a framework of complete phylogenetic information. Tests using supertrees are revealing some patterns for what factors underlie differences in species richness (e.g., Gittleman and Purvis, 1998; Katzourakis *et al.*, 2001; Orme *et al.*, 2002; Salamin and Davies, 2004; Isaac *et al.*, in prep.). For example, the most prevalent hypothesis is that high species richness is associated with small body size because habitats, reproduction, or dietary flexibility will promote high diversity in clades containing small-bodied species. The first phylogenetic test of this hypothesis (Gittleman and Purvis, 1998) was made possible by the existence of the primate and carnivore supertrees, and showed that there was little evidence for an association between body mass and species diversity in these groups.

5. Co-speciation

Interest has focused recently on investigating the patterns of joint speciation of two or more lineages; the best example is that between parasites and their hosts (reviewed in Page and Charleston, 1998; Page, 2003; Figure 3). Researchers are examining how well such lineages track each other; for example, if parasites track their host perfectly, then the respective trees would be expected to be mirror images of one another. If processes other than co-speciation occur, then parasites might switch lineages or speciate independently of the host (Page, 2003). Understanding the patterns of co-speciation can lead to understanding the process of adaptation of parasites and their hosts and the relative rate of evolution of these two clades. For example, Morand *et al.* (2000) demonstrated that louse body size was dependent on the size of their gopher hosts through a lock-and-key relationship that depended upon the thickness of the hair of the gopher and the size of the groove on the head of the louse with which it grips the hair.

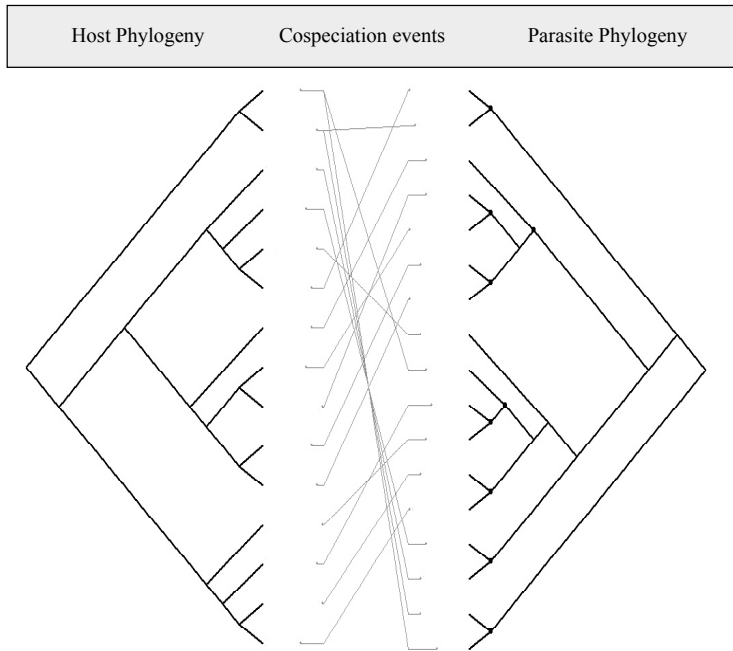


Figure 3. Mapping co-speciation. Estimating the degree of congruence between two phylogenies is possible with complete trees of both clades (e.g., hosts and parasites).

The majority of recent studies seem to indicate a difference in congruence between interacting lineages: congruence is imperfect or absent for most kind of interactions, although there seems to be stronger support for associations between intracellular bacterial symbionts and their invertebrate hosts (e.g., Clark *et al.*, 2000). Complete trees seem to be crucial for these studies to accurately map co-speciation events; these analyses require not just one, but two complete trees. The development of new statistical methods to incorporate the fact that parasites can transfer horizontally onto hosts and that both phylogenies might contain topological errors makes this an exciting area of future research (Charleston, 1998; Huelsenbeck *et al.*, 2003).

6. Community ecology

Interest has grown recently in using phylogenies to investigate ecological community structure (Tofts and Silvertown, 2000; Webb, 2000; Webb and Pitman, 2002; reviewed in Webb *et al.*, 2002). Differences in community structure will reflect not only the similarity of the environments, but also the phylogenetic similarity of the lineages within the two communities. For

example, Webb (2000) compared tree species found within 0.16 ha plots of Indonesian rain forest with species drawn randomly from the species pool. Phylogenetic relatedness of the co-occurring species was found to be higher than that of those selected from random, suggesting some degree of phylogenetic niche conservatism.

In addressing these community level questions, complete trees are less essential than having a tree that covers all the species within the community or its source pool (i.e., species present at a scale larger than the community being studied from which the community can be assembled). However, using complete trees might still be important because species within communities interact on the basis of phenotype, and incomplete taxon sampling could lead to inaccurate inferences of character evolution and assessment of which traits are conserved or homoplastic. Generating such inclusive trees that sample complete communities (“community phylogenies”; Webb *et al.*, 2002) seems viable currently only using supertree construction techniques.

7. Biodiversity and conservation

Species biodiversity is being lost at an alarming rate. For example, according to the latest figures assembled by the IUCN (2002 IUCN Red List of Threatened Species; <http://www.redlist.org>), at least one-third of mammals are threatened with extinction. Applications of complete trees have an important role to play in conservation because they can give some answers to questions that otherwise would not be accessible from traditional phylogenies (Mace *et al.*, 2003). Complete trees that have estimates of taxon divergence times can be used to estimate measures of phylogenetic diversity (*PD*) from the lengths of the branches separating different taxa (Faith, 1992; Nee and May, 1997). Dated supertrees allow a measure of *PD* for a large clade of hundreds of species that would not be possible from other, conventional phylogenies. For example, in the Chiroptera, the bumblebee bat (*Craseonycteris thonglongyai*) is the sole representative of a distinctive family of bats that originated approximately 40 million years ago (Jones *et al.*, in prep.). This species will have a higher measure of phylogenetic diversity, and therefore might be more worthy of conservation effort, than a species of *Myotis* bat which comes from a genus of over 60 species that originated approximately 10 million years ago (Figure 4). These estimates of *PD* can be used in different ways to inform us of the potential impact of the current extinction crisis and to help inform policy makers of the best ways to ameliorate human impacts on biodiversity.

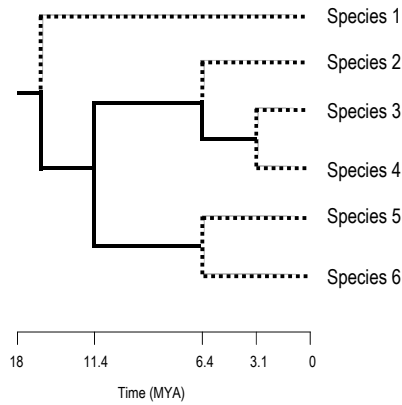


Figure 4. Losing shared and unique evolutionary history. Phylogenetic diversity (*PD*) is shown by the length of the branches (in units of time) joining different species in the phylogeny. *PD* that is shared between all species in the clade is shown in solid lines, whereas *PD* that is unique to each species is shown in dashed lines. The extinction of species 1 would have a greater impact on the phylogenetic diversity of the clade than if species 3 was lost (adapted from Mace *et al.*, 2003).

7.1 Impacts of current extinction crisis

Interest in the potential effects of extinction on the Tree of Life were sparked by a simulation study showing that the majority of phylogenetic diversity in the Tree of Life would be preserved (81%) under specific conditions (e.g., cladogenesis in the form of asymmetric trees and random extinction), even with high numbers of species extinctions (95%) (Nee and May, 1997). However, extinction is not random: closely related taxa share similar levels of threat (Russell *et al.*, 1998; see also Mace *et al.*, 2003), such that when one species is threatened it is probable that closely related taxa in the tree are also threatened. Complete supertrees for primates and carnivores were used to estimate the amount of *PD* lost if species classified as threatened according to the 2002 IUCN Red List of Threatened Species (<http://www.redlist.org>) went extinct relative to random extinction (Purvis *et al.*, 2000a; see also Mooers *et al.*, in press). In primates, but not in carnivores, significantly more *PD* would be lost than expected. Primates have a tree that is more unbalanced than carnivores (many long branches with few species and short branches with many species), thus making the effect of the non-random distribution of threat more pronounced. This points to another crucial reason for using a complete tree: tree balance would not have been possible to estimate, nor would its effects on these results.

7.2 Conservation priority setting

Conservation policy makers are interested in setting priorities in the face of limited resources to minimize the impacts of the human-caused extinction crisis. Many conservation priority-setting exercises are area or species based, focusing on distinctive areas or species to preserve as much biological diversity as possible (i.e., conservation hotspots; Myers *et al.*, 2000). *PD* is another measure of distinctiveness that is starting to be recognized as being important to conservation-policy decisions (Purvis *et al.*, in press). For example, it is important to know how if areas that are important for total numbers of species (species-richness hotspots) are those that also contain the most phylogenetic diversity (*PD* hotspots). Evidence would suggest that these hotspots are essentially overlapping (Sechrest *et al.*, 2002), but more complete dated trees for different clades are needed to address these questions comprehensively. Such trees can be used additionally to indicate the processes that have created the pattern of current biodiversity. For example, the phylogeny could be used to identify rapidly diversifying clades, which combined with geographic information, might enable us to distinguish between “cradles” of diversity from “museums” (Chown and Gaston, 2000; Mace *et al.*, 2003).

8. Caveats to supertree usage

This chapter rests on a key assumption: supertrees are an effective means for procuring complete, large trees that are very difficult, if not impossible, to acquire from traditional methods. Therefore, it is important to assess whether the shortcut of a supertree is indeed effective in the sense of providing phylogenetic accuracy. As described above, there are many exciting reasons to use supertree construction techniques for comparative hypothesis testing. Nevertheless, similar to using phylogenies in general, supertrees can give inaccurate phylogenetic information for comparative studies. The following problems are apparent with the supertrees that have been used thus far; solutions for dealing with these problems are preliminary because we have started using supertrees only recently.

The first issue is whether branch lengths are wrong in dated supertrees (see also Moore *et al.*, 2004). Errors could involve using inaccurate molecular information or when there is clear disparity between molecular divergence times and fossil evidence (assuming the rarity of a molecular phylogeny including fossil taxa). In either case, all comparative tests will suffer from these problems. Another form of error could arise from missing taxa. The influence missing taxa have on a comparative result depends on

where omissions occur in the phylogeny relative to the clade that is being tested. Some diagnostic tests can be performed to investigate lineages-through-time plots to see if there are numerous missing taxa at certain time intervals. If the pattern does not match up with the known extinction patterns for a lineage, then there are probably missing taxa that should be accounted for or tested against alternative trees. Similar to phylogenetic tests in general (Losos, 1994; Martins, 1996; Housworth and Martins, 2001), an analytical solution is to generate alternative phylogenies in which the branch lengths are varied to examine the statistical power of a comparative result.

Perhaps the most worrisome issue results from the “garbage in, garbage out” phenomenon, where conflicting or wrong information is used for supertree construction. There are many statistical methods for diagnosing this problem (Bininda-Emonds *et al.*, 2002), but all involve essentially evaluating the kind of information contributing to uncertainty in the tree topology. The solution, again, is to execute the comparative test against alternative tree topologies to examine what the probability is of incorrect information giving a result. There is another solution, however. When it is known that portions of the supertree are reliable but others are inaccurate, as is frequently the case in supertrees where the relationships of taxa are poorly represented or only in the form of taxonomic rank (see Bininda-Emonds *et al.*, 1999; Salamin *et al.*, 2002), one method is to constrain certain nodes that are reliable and then reorder the remaining nodes through a randomization process (Housworth and Martins, 2001). This process would acknowledge in that some of the tree is useful a comparative analysis, but then assess statistically how different topologies influence a result. Although simulation studies show clearly that using even only a small amount of phylogenetic information is better than none (Gittleman and Luh, 1992; Losos, 1994), the reordering method does not handle error in branch lengths or an expected model of character evolution along the branches.

For comparative tests of particular traits, supertrees might bias results because of the different kinds of information they rest upon. For example, a comparative analysis of brain size evolution testing for differences in rate change across clades could be influenced by a supertree that uses disproportionately more phylogenies based on skull characters than molecular ones. A useful diagnostic would be to assess whether the phylogenies that are influential in a supertree are based on the same traits that are the focus of comparative study.

Finally, inaccuracy within a supertree might not always be detrimental. In the context of using supertrees to catalogue what is known about a taxon phylogenetically, many clades that are known poorly are precisely those that are known poorly in general and the most threatened by extinction (see Mace *et al.*, 2003). For example, across the carnivore supertree, Bremer support

values are the lowest for the Herpestidae, a family of 37 mongoose species, of which little information is available on even body size or geographic range distribution. Supertrees, therefore, can be used to send a forceful and empirical signal about which clades desperately need more study.

9. Future directions

What is the fate of supertrees? Undoubtedly the answer will change as primary sources for phylogenies become assembled more systematically, cover a greater span of characters across clades, and are comprehensive across large taxonomic groups. Admittedly, the future of supertrees might be limited, if not obsolete, when complete phylogenies are achieved by other consensus methods. Yet, we see two areas that might be long lasting for supertrees, even when other sources of phylogenetic material become available. One is the inevitable problem of achieving completeness in studies of planetary biodiversity. About 1.5 to 1.8 million species have been described, with anywhere from 3.6 to 100 million remaining to be discovered (Wilson, 2002). Only a fraction of these are known phylogenetically, even for groups such as the mammals that are very well studied (see Bininda-Emonds *et al.*, 1999; Jones *et al.*, 2002). As species concepts become more blurred (see Agapow *et al.*, 2004), it will be more important to develop a measure of biodiversity that is objective and consistent across diverse clades (Mace *et al.*, 2003). A phylogenetically-based concept will be helpful (Purvis and Hector, 2000; Mace *et al.*, 2003), but only if we have phylogenetic information. As shown above for studies of biodiversity and conservation, supertrees will give us phylogenetic information that is available and, more importantly, tell us which clades are crucial to go and gather this information.

The harshest criticism of supertrees comes from the opinion that consistent, full phylogenies must rely on data compilation methods of characters rather than phylogenies (e.g., Gatesy *et al.*, 2002; Gatesy and Springer, 2004). But what if no single character type (i.e., given gene or region of body) will ever be measured for an entire large clade? This is the case for one ultra-charismatic group: the dinosaurs. Phylogenetic information for dinosaurs will never be complete because they are known unfortunately only from a very fragmented fossil record. Therefore, all phylogenies must be derived from character pieces — the essence of what supertrees are based on from individual phylogenies. If nothing else, a complete supertree of all dinosaurs (see Pisani *et al.*, 2002) will be a legacy contribution of supertrees if it provides the best possible phylogeny of this charismatic group.

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