A data based parsimony method of cophylogenetic analysis

KEVIN P. JOHNSON, DEVIN M. DROWN & DALE H. CLAYTON

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Phylogenies of closely interacting groups, such as hosts and parasites, are seldom completely congruent. Incongruence can arise from biologically meaningful differences in the histories of the two groups, or can be generated by artifactual differences that are merely the result of incorrect phylogenies with weakly supported nodes. We present a method that distinguishes between these sources of incongruence and identifies lineages that are responsible for significant differences between phylogenies. We use the logic of conditional combination in that we first test for statistically significant incongruence using the partition homogeneity test. Then we remove all possible combinations of taxa until a non-significant result of this test is achieved. Finally, we construct a 'combined evidence' phylogeny and then reposition the incongruent taxa. This method produces trees for final comparison using reconciliation methods, but it includes only as many incongruence events as can be statistically justified from the data sets. We apply this method to a host–parasite (gopher–louse) data set and identify many fewer incongruence events than do topology based analyses alone. Our method is broadly applicable to comparisons of phylogenies of interacting taxa, such as hosts and parasites, or mutualists. The method should also be useful for other problems involving comparisons of phylogenies, such as multiple gene trees or cladistic biogeography.

Kevin P. Johnson, Devin M. Drown & Dale H. Clayton, Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112-0840, USA

Kevin P. Johnson, present address: Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820, USA. E-mail: kjohnson@inhs.uiuc.edu

Introduction

Cospeciation is parallel cladogenesis of unrelated taxa that yields congruent phylogenies (Brooks & McLennan 1991). Studies of cospeciation are useful for understanding the evolutionary history of closely interacting organisms. For example, speciation events that are shown to have been concurrent can be used to compare rates of evolution between disparate taxa (Hafner *et al*. 1994; Moran *et al*. 1995; Page *et al*. 1998). Cospeciated phylogenies can also be used to assess the influence of speciation by host taxa on speciation of their parasites (Brooks & McLennan 1991), or mutualists (Moran *et al*. 1993).

Cospeciation has been examined most extensively using host–parasite data sets (Brooks & McLennan 1991; Hoberg *et al*. 1997; Paterson & Gray 1997). These studies show that cospeciation is seldom perfect; few phylogenies show 100% congruence, even when closely associated taxa are compared. Often, identification of the cases of incongruence is of prime interest. In host–parasite systems, true historical incongruence between phylogenies can be caused in at least three ways: (i) horizontal switching of host-specific parasites between unrelated host lineages; (ii) parasite duplication, i.e. speciation of parasites within a non-speciating host lineage; or (iii) sorting events, which include parasite extinction and historical failure of a parasite to colonize a new host lineage.

Two general approaches have been used to test the hypothesis of cospeciation and/or incongruence: tree topology based methods (Brooks 1988; Page 1988, 1990, 1993) and data based methods (Huelsenbeck & Rannala 1997; Huelsenbeck *et al*. 1997). Tree based methods compare the topologies of two phylogenies and ask whether there are more cospeciation events than expected by chance (Page 1988). Chance in this case is defined as independence of the two phylogenies; that is, is the first phylogeny random with respect to the second? Such tree based methods use independence of host and parasite phylogenies (no cospeciation) as the null hypothesis. In contrast, data based methods, such as maximum likelihood (Huelsenbeck & Rannala 1997; Huelsenbeck *et al*. 1997), posit the null hypothesis that data sets from two groups of taxa are consistent with an identical phylogeny underlying each. These methods then assess whether strict cospeciation

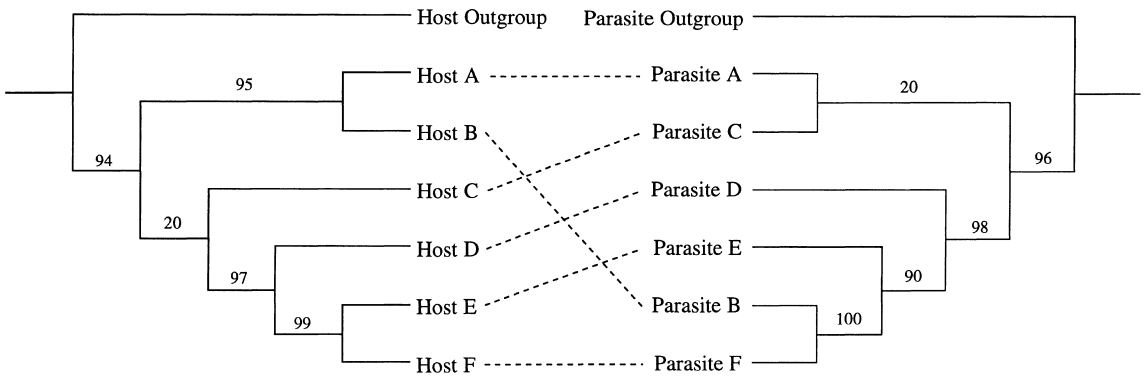

Fig. 1 Hypothetical phylogenies of hosts and their parasites; broken lines indicate host–parasite relationships. Numbers above branches show hypothetical bootstrap values. Note that either placement of B has strong bootstrap support, whereas alternative placements of C are both weakly supported.

can be rejected in favour of a scenario involving incongruence. In this paper, we develop a data based approach using cladistic methods and maximum parsimony in conjunction with the partition homogeneity test.

Much has been written concerning how different data sets should be analysed in phylogenetic studies and how incongruence between phylogenies should be interpreted. Strategies include separate analysis (Lanyon 1993; Miyamoto & Fitch 1995), combined analysis (Miyamoto 1985; Kluge 1989; Barrett *et al.* 1991; Chippendale & Wiens 1994) and conditional combination (Bull *et al.* 1993; deQueiroz 1993; deQueiroz *et al.* 1995). While these approaches have been developed mainly with respect to phylogenies based on different data sets for a single group of taxa (e.g. morphological vs. molecular data, or data for two different genes), the rationale behind these approaches can be extended to examine multiple groups of taxa that may share a common phylogenetic history, such as hosts and parasites.

Incongruence between phylogenies based on different data sets can arise from artifactual incongruence due to weak character support, or significant character incompatibility between alternative character sets (Brower *et al.* 1996). Similar logic can be extended to incongruence between host and parasite phylogenies. That is, differences between host and parasite trees could be due to topological differences between poorly supported nodes, or could result from biologically meaningful incongruence, either statistically significant or not (Bull *et al.* 1993). In the past, differences between host and parasite phylogenies were suggested to be 'real' incongruence (Page & Hafner 1996), even though weak character support of alternative topologies might be a more conservative explanation for some cases. This point is illustrated in Fig. 1, where we show hypothetical host–parasite phylogenies with associated levels of bootstrap (Felsenstein 1985) support. Although the phylogenies are similar, they are incongruent with respect to the placement of B and C. Note that while the incongruent placement of B between phylogenies is strongly supported in bootstrap replicates, the incongruent placement of C between trees is not. Thus, it is more likely that the incongruence involving B is biologically meaningful, whereas that involving C might be more often due to 'sampling error' (Bull *et al.* 1993). What is needed is a method for identifying particular taxa responsible for significant incongruence between phylogenies.

In this paper, we describe a method for determining whether there is significant incongruence between two phylogenies and for identifying which lineages are the source of this incongruence. Our method uses the partition homogeneity test (Farris *et al.* 1994, 1995; Swofford 1998) to test the null hypothesis that host and parasite data sets could be samples of the same underlying phylogeny, as first suggested by Huelsenbeck *et al.* (1997). Because we want to identify incongruence, we must use the alternative, perfect congruence (cospeciation), as the null model. We do this not because we believe that cospeciation is the best null model, but out of statistical necessity. As a further addition to this procedure, we identify specific taxa responsible for incongruence using a taxon deletion methodology. We provide a detailed example of the method using Hafner *et al.*'s (1994) data set on gophers and their lice, and we compare our results with those obtained using other methods.

Methods

The overall approach is to first determine if there is evidence that two data sets (e.g. hosts and parasites) are not samples of the same phylogenetic history (*sensu* Bull *et al.* 1993). If this is the case, then specific taxa with conflicting phylogenetic histories are identified. These conflicting taxa are removed and a 'combined evidence' phylogeny is constructed from the remaining data. The conflicting taxa are then added back to the data sets to reconstruct complete host and parasite phylogenies. Finally, these phylogenies are compared using

reconciliation methods (Page 1994, 1995) to identify the potential events responsible for the significant incongruence.

The initial comparison of host and parasite data sets requires equal numbers of taxa. Therefore, if a host species has more than one parasite species associated with it, the host is duplicated in the host data set. Alternatively, if a parasite occurs on more than one host species, the parasite is duplicated in the parasite data set. These duplications produce an equal number of host and parasite terminals. That is, there is one terminal for each host–parasite association in the data. Trees from the host and parasite data sets are then reconstructed independently to obtain estimates of host and parasite phylogenies.

The partition homogeneity test is then performed (Farris *et al*. 1994, 1995; Swofford 1998) using the host–parasite data sets (informative characters only) as the two partitions. This test determines whether evidence exists for differing phylogenetic histories underlying the two data sets. If the partition homogeneity test indicates significant conflict, a single 'taxon' (host–parasite association) is removed from the data set and the partition homogeneity test is repeated. Simulations indicate that the Type I error rate of the partition homogeneity test is often low, while the Type II error rate can often be quite high (D. M. Drown & K. P. Johnson, unpublished simulations, 2000). Under some conditions, a *P* value cut-off of 0.10 actually represents a Type I error rate of 5% or less. For this reason, a *P* value cut-off of 0.10 is used for purposes of identifying incongruent taxa. This single taxon removal is carried out for each host–parasite association, while performing the partition homogeneity test after each removal. If the *P* value for all of these single taxon removal tests is low (< 0.10), the procedure is repeated for all possible pairs of removed host–parasite associations. If the partition homogeneity test is still significant for all paired removals, the removals are continued for all possible triplets, etc. Once a *P* value for any test exceeds 0.10 for any set of removals (pairs, triplets, etc.), the taxon removal procedure is halted. If more than one test has a *P* value greater than 0.10, the combination producing the highest *P* value is chosen.

The *P* value of the partition homogeneity test is related to the number of additional steps of one data set over the tree of another. If trees from two data sets are identical, the *P* value will always be 1.0; under parsimony, no randomization of data partitions will produce tree lengths longer than the original partitions. In many ways, this is analogous to the partitioned Bremer support (Baker & DeSalle 1997), which calculates the Bremer support for a node for various partitions of the data. The node with the highest absolute values of the differences in partitioned Bremer support are the nodes with the highest incongruence between data partitions. Similarly, the host–parasite associations, when removed, that produce the highest *P* value for the partition homogeneity test in the remaining data are those associations that contain the most incongruence between host and parasite data sets. Again, a high *P* value for the partition homogeneity test indicates no strong evidence for incongruence. The host–parasite associations producing the most incongruence (under a null model of no incongruence) are of interest, and this is the criterion for choosing which host–parasite associations are significantly incongruent between phylogenies. The removal is stopped when a non-significant *P* value (> 0.10) is obtained to be somewhat conservative in identifying incongruent associations. Only those incongruent associations that have statistical support are considered.

The above steps yield two sets of host–parasite taxa. For the first set, restricted to the host–parasite associations remaining in the data set after the taxon deletion procedure, there is no strong evidence to reject perfect congruence. The second set, containing deleted taxa, includes host–parasite associations that are individually responsible for statistically significant incongruence between host and parasite phylogenies. Because perfect congruence for the first set of host–parasite pairs cannot be rejected, a combined evidence topology is constructed for the first set of taxa. This topology depicts a perfectly congruent host–parasite phylogeny. To explore potential explanations for incongruence among the deleted host–parasite pairs, these taxa are added back to the host and parasite phylogenies. The combined evidence topology for the host is constrained (backbone constraint), the deleted host taxa are added back to the host data set, and a parsimony search is conducted. This yields a complete host phylogeny. The procedure is then carried out for the parasite, once again constraining the combined evidence topology to produce a complete parasite phylogeny.

The final step is to reconstruct the minimum number and types of events needed to account for incongruence between the complete host and parasite phylogenies. These events include host switching, sorting events and parasite duplication (Page & Hafner 1996). TreeMap analysis (Page 1994, 1995) is a convenient form of analysis for such explorations.

To work out an example using our method, we used Hafner *et al*.'s (1994) data set for gophers and their lice. We downloaded relevant sequences from GenBank and constructed host and parasite data sets. The data sets consist of 379 bp of the CO I gene of the mitochondrion for the host and parasite. Because the number of characters constituting these data sets is relatively small, it is conceivable that the differences observed between host and parasite phylogenies (Hafner *et al*. 1994) could be due to poorly supported nodes rather than statistically 'real' incongruence. We executed the above procedure (all analyses using PAUP*, Swofford 1998) and compared our results with those obtained by reconciliation and TreeMap analysis (Page & Hafner 1996), and those reported by Huelsenbeck *et al*. (1997) using maximum likelihood ratio tests.

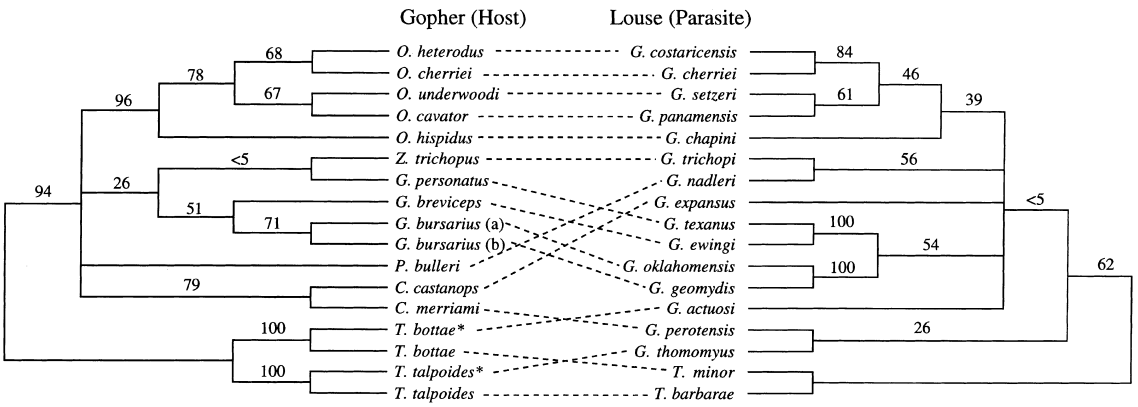

Fig. 2 Strict consensus of phylogenies for gophers and lice using unordered parsimony with CO I mtDNA sequences (Hafner *et al*. 1994). Numbers above branches are bootstrap values. *Duplicated host taxa. Gopher genera: *C.* = *Cratogeomys*, *G.* = *Geomys*, *O.* = *Orthogeomys*, *P.* = *Pappogeomys*, *T.* = *Thomomys*, *Z.* = *Zygogeomys*. Subspecies of *G. bursarius* are (a) *halli* and (b) *majusculus*. Louse genera: *G.* = *Geomydoecus*, *T.* = *Thomomydoecus*.

An example

The gopher–louse data set consists of 15 species and subspecies of gophers parasitized by 17 species of lice (Fig. 2). Most of the gopher taxa have a single species of louse that is found only on that gopher. Two taxa of gophers each have two species of lice. Because the partition homogeneity test requires an equal number of taxa in the two data partitions, we duplicated gopher data for the two taxa with multiple lice to represent each host–parasite association. Our reanalysis of the CO I data set yielded two trees for the gophers and three trees for the lice (Fig. 2). The host and parasite trees were not entirely congruent.

A partition homogeneity test (1000 replicates) revealed that the gopher and louse data sets are unlikely to be samples of the same phylogenetic history ($P = 0.001$), thus rejecting the hypothesis of strict cospeciation. We removed taxa (host–parasite associations) one at a time and repeated the partition homogeneity test. The *P* value was 0.001 (or less) for each of these tests, so we continued to remove all combinations of taxa two at a time, then three at a time, etc., until the *P* value exceeded 0.10. When we removed a combination of four taxa, we found several cases where the *P* value exceeded 0.10 (see Fig. 3). The combination with the highest *P* value (0.733) was the gopher–louse associations *Geomys breviceps/Geomydoecus ewingi*, the duplicated *Thomomys bottae/Geomydoecus actuosi*, the duplicated *Thomomys talpoides/Geomydoecus thomomyus* and *Cratogeomys merriami/Geomydoecus perotensis*. The next highest *P* value was 0.484 and involved the removal of the same gopher taxa as above with the alternative associations for *Thomomys bottae* and *Thomomys talpoides*, involving the louse genus *Thomomydoecus*. At this point in the analysis, no strong statistical evidence remained for the host and parasite data sets being samples of different phylogenetic histories.

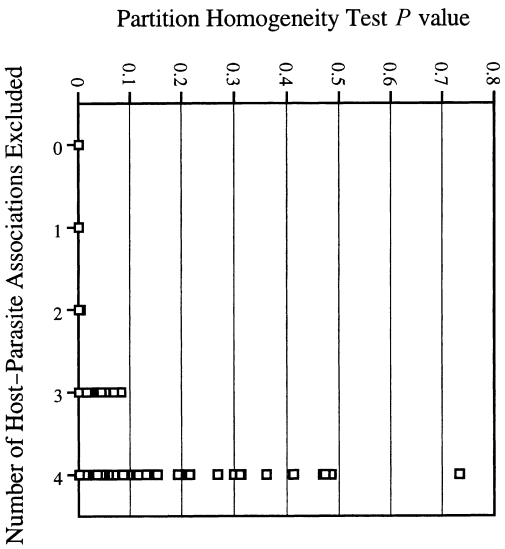

Fig. 3 Plot of *P* values from partition homogeneity tests against number of host–parasite associations removed for the gopher–louse data set. Note that, until four associations are removed, *P* values remain quite low, indicating that four associations must be deleted to remove significant incongruence between host and parasite phylogenies. Number of partition homogeneity tests for each exclusion category: zero, 1; one, 17; two, 136; three, 680; four, 2380.

That is, strict cospeciation could not be rejected for most of the ingroup taxa (11 gopher–louse pairs).

We removed these four pairs of taxa from the host–parasite data set and constructed a combined evidence phylogeny by analysing the data sets simultaneously. This combined evidence phylogeny (Fig. 4) is entirely consistent with the 50%

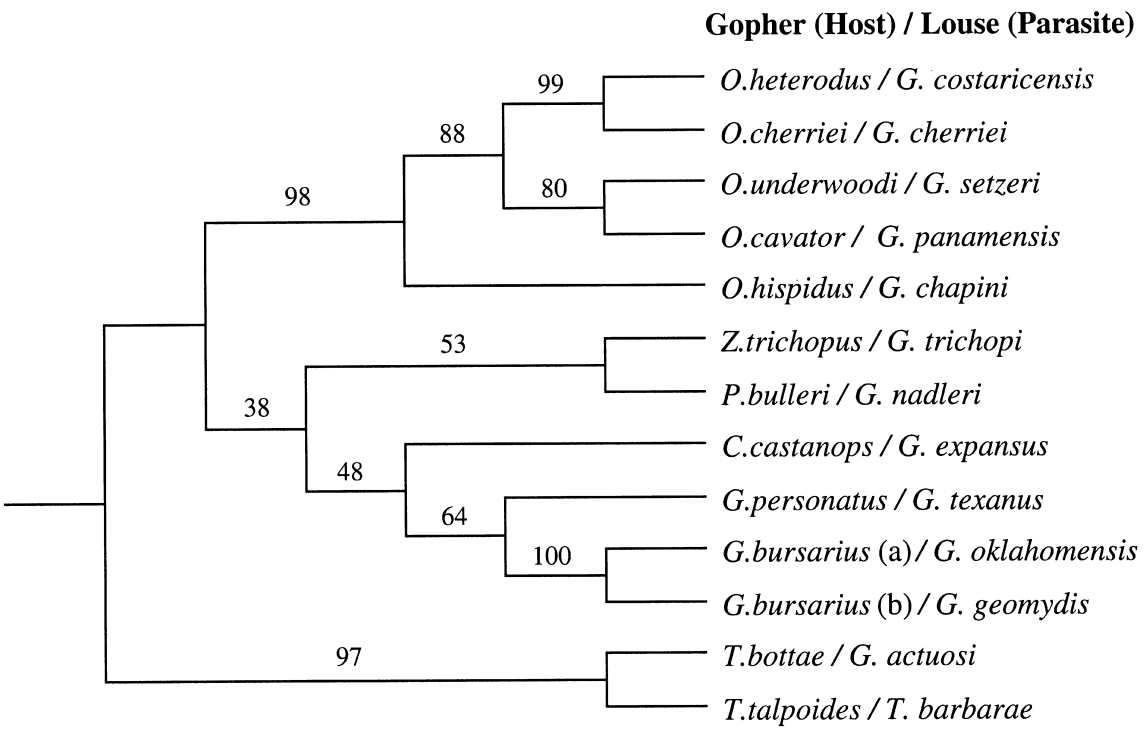

Fig. 4 Combined evidence topology derived by combining gopher and louse data, excluding host–parasite associations that show significant incongruence between data sets based on the partition homogeneity test and the taxon deletion procedure. Numbers above branches are bootstrap values from the combined analysis. Note support for nodes in common to host and parasite trees has increased from Fig. 2. Conventions as in Fig. 2.

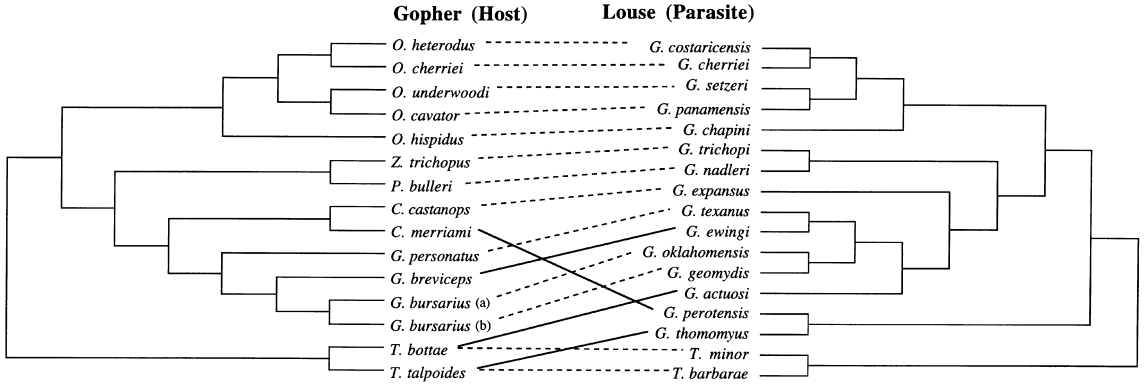

Fig. 5 Phylogenies for gophers and lice after taxa showing conflict have been added back to the constrained, combined evidence topology (Fig. 4). Bold lines indicate four host–parasite associations that are significant sources of incongruence between data sets. Conventions as in Fig. 2.

bootstrap topologies of the two data sets analysed separately. To evaluate patterns of incongruence between the gopher and louse phylogenies, we constrained the combined evidence topology, added back the previously removed gopher and louse taxa, and analysed each data set separately. This procedure produced new phylogenies (Fig. 5) for both hosts and parasites, and minimizes the number of incongruent nodes as can be statistically justified.

Reconciliation analysis, which assumes no host switching (Page 1990), recovered 10 cospeciation events and required six duplications and 23 sorting events. TreeMap analysis (Page 1994, 1995), which allows for host switches, recovered

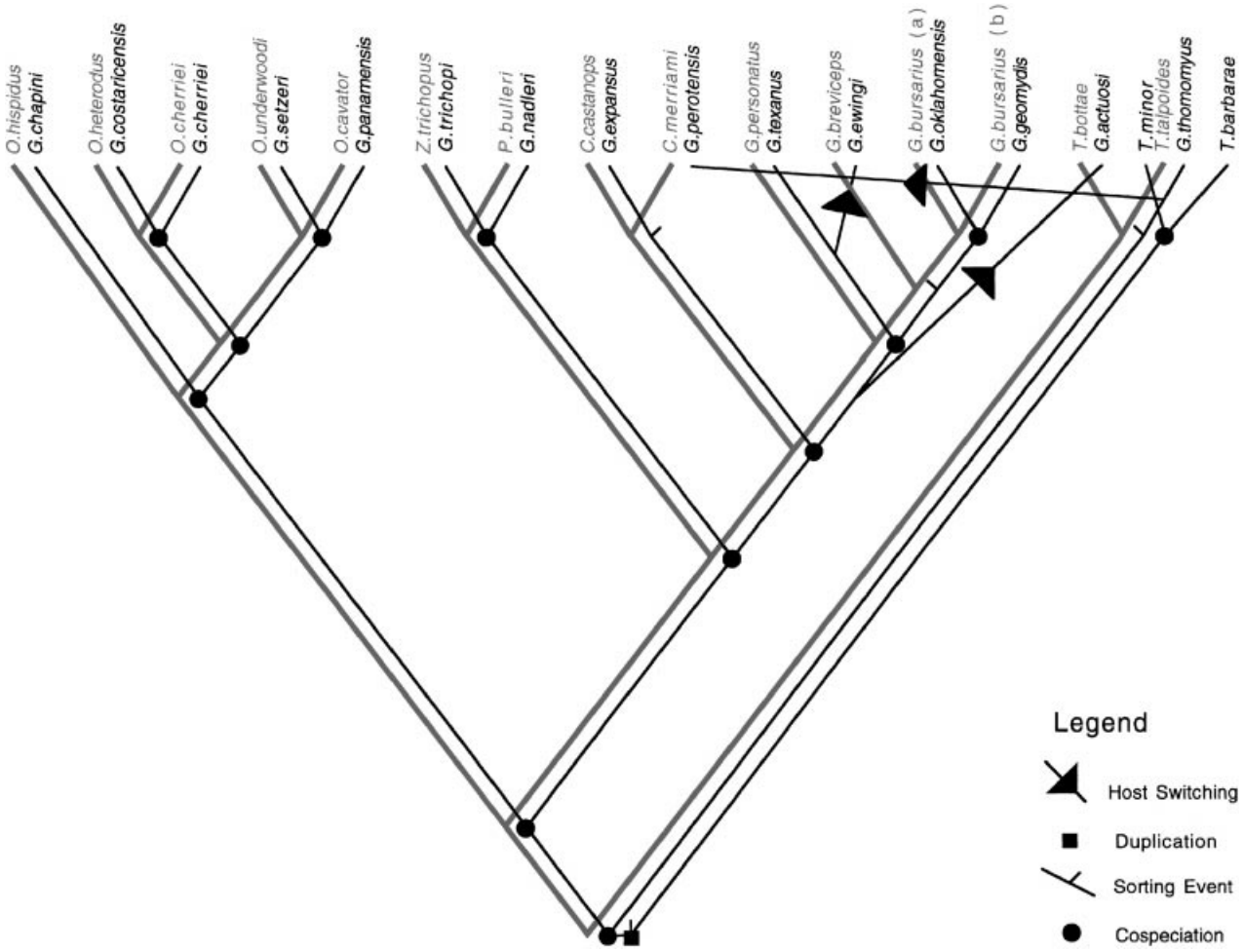

Fig. 6 A historical scenario of cospeciation and 'incongruence events' resulting from a TreeMap (Page 1994, 1995) analysis of gopher and louse phylogenies. One duplication event, four sorting events and three host switching events are depicted. Conventions as in Fig. 2.

12 cospeciation events and produced two scenarios involving eight events to explain the incongruence (one scenario is shown in Fig. 6). In both scenarios, there were three host switches, one duplication and four sorting events. Most reconstructions (e.g. Fig. 6) suggest that one member of the louse ingroup (in this case *Geomydoecus actuosi*) switched hosts onto *Thomomys bottae*. In the reconstruction shown in Fig. 6, a duplication event took place early in the history of the gopher–louse radiation, with subsequent incongruence events (sorting and host switching) occurring in the ingroup to produce the pattern of host–parasite association.

Discussion

Our method generates host and parasite trees that are minimally incongruent. The method postulates incongruence only when there is statistical evidence for incongruence. In contrast to tree based methods (Brooks 1988; Page 1990, 1993), our approach directly includes the possibility of artifactual incongruence due to conflict between poorly supported nodes. Not surprisingly, the number of cospeciation events recovered by our method is higher than that recovered by tree based methods; conversely, the number of 'incongruence events' is lower. These cospeciation events represent an upper bound on the amount of cospeciation consistent with the data. The actual number of cospeciation events might often be less than this upper limit. Because in this method we use cospeciation as a null model for statistical purposes, we cannot evaluate instances of cospeciation. Rather, our method succeeds by identifying incongruence events that are strongly supported by the data.

Page & Hafner's (1996) reconstruction using the gopher–louse data indicated 10 cospeciation events (vs. 12 in our analysis) and required 26 incongruence events. They presented a reconstruction involving one host switch, five duplications

and 20 sorting events. In our analysis, only eight incongruence events were needed to reconcile the host and parasite phylogenies (three host switches, one duplication and four sorting events). Other reconciliations are possible; however, the number of incongruence events with our method will invariably be lower than or equal to that recovered by tree based reconciliation methods.

Huelsenbeck *et al.* (1997) used a data based maximum likelihood approach to evaluate incongruence between the gopher and louse data sets. Like our data based parsimony approach, their approach recovered statistically significant incongruence between the gopher and louse data sets. Huelsenbeck *et al.* (1997) identified a small clade of five host–parasite pairs for which there was no evidence of incongruence (also found in our analysis); however, they did not identify the taxa responsible for the incongruence (although this might be possible by extending their maximum likelihood method). Although Huelsenbeck *et al.* (1997) estimated the amount of host switching compatible with the phylogenetic incongruence, they did not directly identify events causing incongruence between phylogenies. Our method identifies the taxa (associations) responsible for the incongruence and allows a new reconstruction of host and parasite phylogenies with which reconciliation analysis (Page 1990) or TreeMap analysis (Page 1994, 1995) can then be conducted.

While the data based maximum likelihood method of Huelsenbeck *et al.* (1997) is useful for testing hypotheses relating to host–parasite coevolution, our method offers some advantages over their method. Maximum parsimony generally requires much less computing time than maximum likelihood. Although this may not be an issue with relatively small data sets, computing power may severely limit maximum likelihood based methods for larger data sets. Furthermore, Huelsenbeck *et al.* (1997) did not explicitly treat hosts with multiple parasites other than exclude them from the analysis (although they did suggest that these taxa might be duplicated, as we have done). Excluding taxa has the disadvantage that these taxa are the most likely candidates for incongruence events, which are important events for evaluating the complete history of coevolutionary relationships. Two of the four cases of incongruence in our analysis involved the two cases in which more than one louse was found on a single host taxon.

Another method that might have potential to incorporate phylogenetic uncertainty into cophylogenetic analysis is parsimony based tree fitting (Ronquist & Nylin 1990; Ronquist 1995, 1998). In this method, costs are assigned to cophylogenetic events. As currently implemented, this method does not take tree uncertainty into account. However, a global analysis taking into account both tree length costs (from character matrices) and cophylogenetic event costs could assess tree structures consistent with both underlying phylogenetic data and cophylogenetic events. Future application of such a method requires information on relative weights as well as computational implementation.

Limitations of our method

While our method has several advantages over previously developed methods, we acknowledge several limitations. When there is little actual cospeciation, the method may be difficult to implement. When more than half of the taxa are incongruent between hosts and parasites, our method will likely have difficulty identifying exactly which taxa are responsible for incongruence. For this reason, it is a good idea to begin by examining topological incongruence using Page's (1988) method, which tests whether two phylogenies are more similar than expected by chance. If the null hypothesis cannot be rejected using Page's method (given enough data to provide reasonably well-resolved phylogenies), then use of our method is not warranted since it posits a null hypothesis of perfect congruence. For the gopher and louse data, there is strong evidence (Page & Hafner 1996) for at least some topological congruence, so it is reasonable in this case to proceed with our method.

A further difficulty relates to incongruence involving large clades deep in the phylogeny. In the case of incongruence deep in the host–parasite phylogenies, our method will correctly identify this incongruence. However, the entire clade involved in the significant deep incongruence will be excluded from further analysis and will simply be put back into the phylogeny at the constraint step. Thus, any incongruence within such a deep clade will not be analysed further. In cases where an entire deep clade is identified for exclusion, we suggest repeating the procedure with just this clade in the analysis to identify possible causes of incongruence within such a clade.

Another limitation of our method is that, like other data based methods, it requires character based data sets for both the hosts and parasites. This is also a requirement of maximum likelihood approaches but not topological approaches. For example, a comparison of topologies could still be conducted using phylogenies derived from distance based data with neighbour joining. However, such comparisons do not control for the possibility that the number of incongruence events will be overestimated due to artifactual topological incongruence between distance based trees.

Conclusions

Data based methods for examining incongruence, such as maximum likelihood or parsimony, can shed light on numerous problems in phylogenetic systematics. In cophylogenetic studies, it is important not only to identify whether significant differences exist between host and parasite phylogenies, but also to identify which taxa exhibit incongruence. For example, if host switching is inferred for a

taxon, the question of why that particular taxon might have switched hosts can be addressed comparatively and experimentally (Page *et al*. 1996).

Our method is not restricted to cophylogenetic analysis of interacting taxa. The method can also be used to examine incongruence between data sets concerning the phylogeny of a single group of taxa. Much of the topological conflict between phylogenies derived from different data sets can be due to 'sampling error' (Bull *et al*. 1993), but significant, biologically meaningful conflict can also be involved. For example, horizontal gene transfer (deQueiroz 1993) or uneven lineage sorting events (Pamilo & Nei 1988) can cause phylogenies from two or more genes to differ. Our method can be used to identify which taxa are involved in a horizontal gene transfer event. As another example, non-independence within a data set, e.g. due to convergence, can cause phylogenies estimated from alternative data sets to show significant conflict. In such cases, our method has the potential to identify which taxa are involved in this non-independence, thus allowing character states for these taxa to be examined more carefully (e.g. Johnson & Sorenson 1999).

Yet another use for our method is in developing area cladograms under vicariance biogeography using phylogenies of different taxa (Page 1988; Wiley 1988). Topology based approaches (Page 1988) do not consider weak support for conflicting nodes as a possible explanation for differences in area cladograms. In such cases, a combined evidence area cladogram, analogous to our combined evidence host–parasite tree, can be constructed. Taxa deleted in our procedure are candidates for dispersal between geographical areas.

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