

## Book review

### TANGLED TREES: PHYLOGENY, COSPECIATION, AND COEVOLUTION

Edited by Roderic D. M. Page

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Both coevolution (reciprocal selection among interacting organisms) and cospeciation (parallel speciation of two interacting lineages) are intrinsically appealing concepts. This is because we often encounter extraordinary specialisations in one organism that appear to result from interactions with another organism. Furthermore, the implicit neatness of two lineages diverging synchronously ensures that coevolution and cospeciation remain attractive concepts to biologists. But are these concepts deceptively appealing? Both the biological reality and hence the analytical methodology are messier and more complex than theory suggests. When is it coevolution, when is it cospeciation, and when is it something altogether different? Rod Page's introduction provides a succinct summary of the 'what', 'why' and 'when' of cospeciation. He also goes some way to clarifying and delimiting these concepts, but concedes that 'terminological pluralism' is common.

*Tangled Trees* illustrates how important the development of phylogenetics has been to the analysis of historical processes. Coevolution and cospeciation are concepts that have been around for a long time. The more recent application of phylogenetics to the analysis of these concepts has opened up something of a biological and methodological Pandora's Box. This is partly reflected in the multiplication of terminologies, and partly evident in the increasing complexity of algorithms needed to approximate the historical 'reality'. Phylogenetic reconstructions are a powerful means to explore historical associations, but they also bring additional complexity and limitations inherent in the construction of phylogenetic hypotheses. Some of the chapters in this book explicitly address these challenges.

The main themes of *Tangled Trees* are the detection of patterns indicative of cospeciation, and the reconstruction of historical events in host–parasite interactions. There are limitations inherent in interpreting any historical process. Not least is that we usually only have information from extant taxa because interactions between organisms rarely fossilise. In addition, the dynamic nature of biological interactions makes reconstruction and analysis more difficult with increasing time. As editor, and organiser of the symposium at which many of the authors presented the

research published here, Page has gathered together those eminently qualified to explain the latest developments, limitations, and future directions of research in this field. Several of the chapters are authored by those actively developing methods and programs to analyse historical interactions. These authors provide revealing insights into the computational problems and shortfalls of different approaches (e.g. parsimony versus likelihood methods, and the challenges of incorporating phylogenetic uncertainty). Page likens the search for an overarching methodology for reconstructing historical associations (genes in species, parasites on hosts, species in geographical areas) as 'the holy grail for theoreticians'. It would be exciting if these developments allowed for the incorporation of multiple interacting lineages (e.g. tritrophic interactions) in a single analysis – a 'jungle' of genes, parasites, hosts and areas, which could be used to analyse the divergence of each on the other. The rapidity with which comparatively sampled data sets of interacting organisms can now be generated using molecular techniques will provide many challenges to the sophistication of the analytical tools reviewed in this book.

*Tangled Trees* includes twelve chapters divided under two headings: 'Theoretical Issues' and 'Empirical Examples'. The empirical examples are biased towards animal host–parasite systems, with no plant host–parasite studies included. However, this omission (acknowledged by Page) does not detract from this book as the only up-to-date synthesis of approaches and methodologies. The study systems in both theoretical and empirical chapters use mammals, birds, reptiles, nematodes, viruses, and, of course, lice. The predominant focus on lice reflects the historical role played by these insects in the formulation of the governing principles, or 'rules', of parasitism set by Fahrenholz and Eichler (reviewed in Klassen 1992). There is also the classic gopher–louse study, which became an early model of cospeciation using phylogenetic reconstructions (Hafner and Nadler 1988).

Currently, methods for detecting cospeciation reconcile two phylogenies of interacting organisms and then use various optimisation or likelihood schemes to determine the type and number of events (e.g. cospeciation, host switching, speciation in one lineage without reciprocal speciation in the other), which are required to explain the observed patterns of association in extant taxa. No methods have yet been developed to incorporate additional biological complexities such as different stages in parasite lifecycles (e.g. parasites with multiple hosts). For reasons discussed in detail in several chapters, and also in Charleston (1998) and Legendre *et al.* (2002), detecting cospeciation becomes more problematic as relative levels of host-switching events increase and programs for analysing the extent of cospeciation (e.g. TreeMap, TreeFitter, ParaFit) become less optimal as cospeciation becomes less common. Significant

levels of non-random associations that are due to events other than cospeciation, such as resource tracking or phylogenetically conserved host switching, may be confounding and prove difficult to differentiate from 'true' cospeciation. Indeed, cospeciation may be less frequent than expected even among highly specialised animal parasites, as discussed in the chapter by Taylor and Purvis on the diversification of mammals and their chewing lice, and in the chapter by Charleston and Perkins (which demonstrates the advances implemented in 'jungles': TreeMap 2) using Caribbean lizards and their malarial parasites: 'it may be that we are overestimating the degree to which phylogenies should match'. If high levels of cospeciation are only found in select groups of parasites (such as some exemplar louse groups or the endosymbionts of insects) then, to be more broadly applicable, future methods need to focus on detecting genuine but rare cospeciation events in messier interactions.

The critical implications of phylogenetic uncertainty in interpreting historical events are acknowledged by most of the contributors but only tackled methodologically in one chapter by Huelsenbeck *et al.* in which they implement Bayesian statistical measures of uncertainty. Another important issue, central to the concept of cospeciation, is the chronology of putative events and temporal synchronicity. Identical patterns of phylogenetic congruence could be due to cospeciation if contemporaneous, but must be due to other factors if not. The chapter by Demastes *et al.* considers the effects of different evolutionary rates in host and parasite lineages and the complexity introduced by spatial and temporal heterogeneity in recently diverging groups. The chapters by Charleston and Perkins and Huelsenbeck *et al.* discuss the methodological implications of temporal synchronicity, but it seems that more robust methods of testing for temporal congruence as well as the incorporation of different sources of temporal information (e.g. molecular clocks, geological and fossil data) are needed in future analyses.

The interesting biological questions concerning the processes behind the patterns of interaction are discussed in several chapters. Hafner *et al.* point out that even in long-term studies our knowledge of the root causes of host specificity and the implications of ecological interactions is

often slight. Paterson *et al.* emphasise that in all cases of cospeciation analysis, the biological, geographical and ecological reality of the observed patterns needs to be critically assessed. Rannala and Michalakis consider the effects of population demographics (migration and genetic drift) on analyses of congruence between species, genes, populations and individuals. Johnson and Clayton and Clayton *et al.* examine the usefulness of comparative methods using ecological replicates (wing and body lice on birds), and they illustrate the potential for interpreting macroevolutionary patterns by extrapolating back from the observed ecology of extant taxa. Future developments will undoubtedly include more realistic interpretations of non-cospeciation events, tests of temporal congruence, and incorporation of phylogenetic uncertainty. But promising mathematical and statistical developments aside, perhaps the most exciting future directions are encapsulated in the final chapter by Clayton *et al.* on the 'potential synergy between ecological and cophylogenetic studies'.

*Tangled Trees* is a most welcome synthesis. It not only explains in detail the methodologies available for analysing complex interactions between host and parasite organisms over time, but also clearly illustrates how the detection of historical cospeciation events may be confounded by processes such as incomplete lineage sorting, extinction and host switching. This book excellently summarises the achievements that have been realised in the complex field of cospeciation analyses, and raises many challenges for future research.

## References

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