

## Using Tree Shape

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Although the primary purpose of phylogenies is to depict evolutionary relationships among taxa, they have other interesting properties. One of the most interesting is their shape, some quantifiable measure of how they look. Such measures come in two general flavors: diversity variation among contemporaneous clades (e.g., when averaged over the whole tree, this is tree balance) and distribution of splitting times (e.g., lineages-through-time plots). These measures represent variation in diversification rates among taxa at a given time and within a taxon through time, respectively. As such, tree shape is the signature of the forces that produce biodiversity, and its study informs one of the major areas in evolutionary biology.

It has been over a decade since Craig Guyer and Joseph Slowinski (Slowinski and Guyer, 1989; Guyer and Slowinski, 1991, 1993) began the current era of tree shape work (for a history and general review, see Mooers and Heard, 1997). The concept was elegant: compare shapes of published trees with expectations from reasonable null models, deal with uninteresting technical confounds, and interpret what remains with an eye to explaining past and (perhaps) predicting future diversification (though we might not have called it that a decade ago). A decade on, it is well established that trees shapes contain interesting and important information about the evolutionary process (see, e.g., Gaston and Spicer, 1998; Schluter, 2000; Felsenstein, in press). For the 2001 joint SSB/SSE/ASN meeting, we were fortunate to be able to organize a symposium titled “Developing uses for phylogenetic tree shape in the study of evolution,” an opportunity to organize the decade’s work and foster collaboration for the future. Collected here are papers representing many of the contributing authors and others who presented related material in other sessions of that 2001 meeting. We gratefully acknowledge the support of the Society

of Systematic Biologists, which both sponsored the symposium and agreed to review these papers for publication.

These papers are an excellent, if incomplete, update on the decade’s work on tree shape. As expected, the descriptive aspect has become more sophisticated, with new software tools and ever better statistical power (contributions in this issue by Agapow and Purvis, and Chan and Moore; see also McKenzie and Steel, 2000; Stam, 2002). We are getting better at incorporating and analyzing branch length information (the latest update and extension is by Pybus et al., this issue). There are also some new observations: perhaps the most intriguing is the idea that species-level and higher level phylogenies might actually differ in shape (Purvis and Agapow, this issue). Along with these changes is a welcome expansion into new fields. Two sampled here are comparative methods (a potentially powerful way to summarize tree shapes is presented by Martins and Housworth, this issue) and community structure (Webb and Pitman, this issue). An important distinction between neontological and paleontological phylogenies has been recognized, and tools for dealing with the latter have been developed (Harcourt-Brown, this issue). Finally, Alan de Queiroz submits a provocative essay on the complexity of the question of why some taxonomic groups might diversify more than others.

But we have still just begun. The patterns are certainly real and are becoming better documented (Purvis and Agapow, and Savolainen et al., this issue; Stam, 2002), and the evolutionary models are inching towards increased realism (Heard and Mooers, this issue). However, present explanations for non-random tree shapes are incomplete, and the application of tree-shape concepts in related disciplines is still in its infancy (see, e.g., Heard and Mooers, 2000; von Euler, 2001). We expect to see major advances made with

this deceptively simple but conceptually rich approach.

#### DEDICATION

On behalf of the contributing authors, we are honored to dedicate this symposium collection to the memory of one of the associate editors of *Systematic Biology*, Joseph B. Slowinski, who died 12 September, 2001 at the age of 39. Joe Slowinski was not the first biologist to publish on phylogenetic tree shape, nor was tree shape his primary research emphasis. However, in the late 1980s and early 1990s, Joe published three major papers with Craig Guyer (Slowinski and Guyer, 1989; Guyer and Slowinski, 1991, 1993) that played an important role in inspiring and shaping the subsequent proliferation of work on tree shape. Among the strengths of this work were a strong statistical framework and the close connection drawn between tree shape and major macroevolutionary questions about the origin of Earth's biodiversity.

Tree shape was only one of Joe Slowinski's research interests. He was an accomplished systematist of snakes (see, e.g., Slowinski and Keogh, 2000; Slowinski et al., 2001), made important methodological contributions with respect to systematic analysis of molecular data (see, e.g., Slowinski, 1998, 2001), and was broadly interested in connections among systematics, molecular evolution, and biological diversification (see, e.g., Zink and Slowinski, 1995; Slowinski and Arbogast, 1999). Joe Slowinski died while collecting snakes in Myanmar; he was bitten by a krait at a remote collection site and died before medical help could reach him. His death saddens those who knew him personally, of course, but also those who knew him only through his work. We hope he would have been pleased to see the appearance of these papers, which are only part of a continuing research enterprise that owes a significant debt to Joe's ideas.

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