

Chapter 14: What have we learned from the trees?

Section 14.1: The Lorax

In Dr. Seuss's "The Lorax" there is a quote that seems appropriate to begin my final chapter.

'Mister,' he said with a sawdusty sneeze,
'I am the Lorax, I speak for the trees.
I speak for the trees, for the trees have no tongues."

From Seuss (1971).

Comparative methods have been rushing forward at breakneck speed to "speak for the trees" for more than 20 years now. At the same time, we have gained more information about the shape of the tree of life than any time in the history of the planet. So, what have we learned so far? And what can we learn moving forward? Perhaps most importantly, how can we overcome the perceived and actual limits of comparative approaches, and enable new breakthroughs in our understanding of evolutionary biology?

Section 14.2: What we have learned so far

The great success of comparative methods has been, I think, in testing hypotheses about adaptation. A variety of methods can be applied to test for evolutionary relationships between form and the environment – and, increasingly, organismal function. These methods applied to real data have shed great light onto the myriad ways that species can adapt. This has been a great boon to organismal biology, and comparative methods are now routinely used to analyze and test hypotheses of adaptation across the tree of life. Methods for detecting adaptation using comparative approaches are growing increasingly sophisticated in terms of the types of data that they can handle, including massively multivariate gene expression data, function-valued trait data, and data from genome sequencing. One can only expect this trend to continue.

One thing seems certain after a few decades of comparative analysis: the tempo of evolution is incredibly variable. Rates of evolution vary both through time and across clades, with the quickest rates of both trait evolution and speciation thousands of times faster than the slowest rates. We can see this variation in analyses from relatively simple tree balance tests to sophisticated Bayesian analyses. So, evolution does not tick along like a clock; instead, rates of evolution depend strongly on lineage, time, and place. The details of these relationships, though, remain to be deciphered.

Comparative methods have played a critical role in our understanding of speciation. Studies using lineage-through-time plots have greatly enhanced our knowledge of diversification rates, and a wide range of results have shown increasing evidence for diversity-dependence in speciation (though this interpretation is not without controversy!). This set of studies provide a nice complement to paleobiological studies of diversification rates using the fossil record.

We can already gain some new biological insights as comparisons among clades start to hint at which factors are responsible for the fact that some species are so much more diverse than others. Perhaps for psychological reasons, most studies have tried to determine explanations for the fastest rates of speciation, as seen in young diverse clades like African cichlids and Andean plants. However, given the high potential for speciation and splitting to accumulate species in a geographic landscape, it might be true that the depauperate clades are really the mysterious parts of the tree of life. Many current research programs are aimed directly at explaining differences in diversity across both narrow and broad phylogenetic scales.

Overall, I think it is easy to see why comparative methods have risen to their current prominence in evolutionary biology. Phylogenetic trees provide a natural way to test evolutionary hypotheses over relatively long time scales without requiring any direct historical information. They have been applied across the tree of life to help scientists understand how species adapt and multiply over long time scales.

Section 14.3: Where can we go next?

As emphasized by Harvey and Pagel (1991), comparative methods have proven to be an essential tool in identifying and describing adaptations. However, the scope of comparative methods has broadened, and now seeks to address broad and long-standing theories of macroevolution. It is in this area that I think comparative methods has promise, but awaits new developments and ideas to really make progress towards the future.

The main challenge, I think, is in identifying and testing broad theories of macroevolution. Too many papers focus on “classic” verbal models of macroevolution – many of which have been defined in contradictory ways over the years and can never really be tested. At the same time, new quantitative theories of macroevolution are lacking.

Let me explore this in a bit more detail using the idea of adaptive radiation and the related concept of ecological opportunity. Perhaps, the theory goes, occasionally lineages enter a new adaptive zone full of niches just waiting to be occupied; the lineage then evolves rapidly to fill those niches. Based on this definition, there are several sets of criteria that one might apply to decide whether or not a particular lineage has experienced such an adaptive radiation.

There are a few alternatives that are sometimes contrasted to this pattern, like nonadaptive radiation.

The concept of adaptive radiation has been very fruitful for inspiring creative and interesting work on model clades, but (in my opinion) we have mostly failed in terms of really predicting adaptive radiations and separating the phenomenon from ‘normal’ evolution. For example, most studies identify lineages undergoing adaptive radiation a priori. Even when the goal is to identify adaptive radiations, some criteria seem hard to pin down; for example, one can require evidence of adaptation, but surely every lineage on the planet has underwent selection and adapted in at least some way over its history. Likewise, we can require common descent, but there is only one tree of life on Earth (that we know!), so eventually one will find that as well. And authors differ dramatically on whether or not adaptive radiations need to be rapid relative to trait evolution and/or lineage diversification in other lineages. Finally, although a few studies have been able to characterize the unique features of adaptive radiations compared to their close relatives, comparisons across broader sections of the tree of life have mostly failed. We still do not know for certain if there is anything that links the “classic” adaptive radiations (e.g. anoles, Darwin’s finches, mammals) and distinguishes them from evolution in normal clades.

Comparative methods have cast doubt on another cornerstone of macroevolution, that of punctuated equilibrium. As we have argued, comparative methods have had varying success in tackling each of the parts of PE theory, but we can see little evidence to link them into a cohesive whole. For one thing, there is too much evidence that lineages adapt and evolve along branches of phylogenetic trees, rather than just at speciation. Quantitative tests do tend to find some statistical support for the idea that change depends on both anagenetic rates and speciation, but “pure” punctuated equilibrium is increasingly hard to defend.

As for other major macroevolutionary theories, some have received mixed support (e.g. Dollo’s law, escape-and-radiation, cospeciation, key innovations), while others have hardly been tested in a comparative framework, probably due to a lack of methods (the geographic mosaic theory, holey adaptive landscapes).

Section 14.4: A hint at the future of comparative methods

It is perilous to predict the future progress of science. Nonetheless, I will offer a few suggestions that I think might be productive avenues for future work in comparative methods.

First, I think comparative methods can and should do a better job of integrating diverse data into a coherent framework. For example, despite clear connections, neither fossils nor contemporary data on the tempo and genetics of speciation typically can be integrated with phylogenetic studies of diversification. Research projects with the same goal, like estimating when and why a lineage undergoes

speciation, are better integrated than separate. There are a few hints about how to proceed: first, speciation models that we fit to both phylogenetic and fossil data must be better connected to the process of speciation; and second, analyses need to consider both paleontological and phylogenetic data simultaneously.

Second, it is absolutely essential to fully deal with uncertainty through entire pipelines of comparative analysis, from tree building to model fitting. The easiest way to do this is through a single integrated Bayesian framework, although using each step's posterior as a prior is nearly as good. Even if one is not a Bayesian, I think it is critical to test how tree uncertainty might affect the results of our comparative analyses.

Third, comparative methods require a more diverse set of models that connect better to biological processes. Current models like Brownian motion and OU have, at best, a weak and many-to-one connection to microevolutionary models. Other models are even more abstract; nothing we can measure about an evolving lineage from one generation to the next, for example, can inform us about the meaning of the lambda parameter from a PGLS analysis. This can be fine statistically, but I think we can do better. The easiest connections to make are between comparative methods and quantitative genetics; in this book I explore only the most basic aspects of this connection. More could, and should, be done. In particular, no trait models that I know of deal with differences in abundance and range size among species, even though these vary tremendously among even very close relatives and are almost certain to affect the tempo and mode of trait evolution.

Section 14.5: Summary

Comparative methods occupy a central place in evolutionary biology. This is because phylogenies provide an accounting of the historical patterns of evolution and, in turn, provide a natural way to measure long-term evolutionary dynamics. The first phase of comparative methods was focused strongly on adaptation. As discussed in this book, we have now branched out into a wide number of new areas, including diversification, community ecology, quantitative genetics, and more. This expansion has involved new statistical approaches that increase the flexibility of comparative methods and their connection to biological processes. I expect this trend to continue, fueled by the creativity and energy of the next crop of young scientists.

Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press.

Seuss. 1971. *The lorax*. Random House.