



## Testing hypotheses in macroevolution



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### ABSTRACT

Experimental manipulation of microevolution (changes in frequency of heritable traits in populations) has shed much light on evolutionary processes. But many evolutionary processes occur on scales that are not amenable to experimental manipulation. Indeed, one of the reasons that macroevolution (changes in biodiversity over time, space and lineages) has sometimes been a controversial topic is that processes underlying the generation of biological diversity generally operate at scales that are not open to direct observation or manipulation. Macroevolutionary hypotheses can be tested by using them to generate predictions then asking whether observations from the biological world match those predictions. Each study that identifies significant correlations between evolutionary events, processes or outcomes can generate new predictions that can be further tested with different datasets, allowing a cumulative process that may narrow down on plausible explanations, or lead to rejection of other explanations as inconsistent or unsupported. A similar approach can be taken even for unique events, for example by comparing patterns in different regions, lineages, or time periods. I will illustrate the promise and pitfalls of these approaches using a range of examples, and discuss the problems of inferring causality from significant evolutionary associations.

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### 1. Experiments in deep time

*“The fact that we expect our theories to have exceptions makes it hard to test them... It makes me envious of my colleagues in molecular biology. They can usually settle their problems by experiment: I seem to live with mine. Of course, my problems are more interesting.”* John Maynard Smith (1990) Taking a Chance on Evolution, New York Review of Books, June 14 1990.

I once had a postprandial argument with a fruitfly geneticist. He said that the work of comparative evolutionary biologists such as myself was all well and good, but it was not real science, because the gold standard of science was the manipulative experiment. If you don't set up a replicated experiment where you apply a treatment to some but not all samples then observe any difference between treatment and controls, then you aren't really doing science,

because any other approach does not allow you to make causal statements. While this “manipulationist” attitude toward establishing causality is less popular with many philosophers of science, it is still promulgated by some experimental scientists, as my conversation with the *Drosophila* geneticist demonstrates (Woodward, 2013). Setting aside the problem of making causal statements from the results of experiments, which is trickier than it first appears, is his statement about comparative evolutionary biology fair?

Experiments in evolution have a long history (de Varigny, 1892). For example, in the 1880's William Dallinger showed that it was possible to increase the thermal tolerance of microbes over many generations by selecting for slight increases each generation, such that the organisms sampled from the end of a multigenerational selection experiment could tolerate high temperatures that would have killed all individuals from the first generation. Experiments on evolutionary change such as this one have built an important body of work in population genetics and behavioural ecology (Buckling, Maclean, Brockhurst, & Colegrave, 2009).

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But there are many evolutionary phenomena that we might wish to study that are not open to experimental manipulation. Here it is helpful to make a distinction between microevolution and macroevolution. Definitions may vary, but I will consider that microevolution describes changes in the relative frequency of heritable traits in a population over generations. On the assumption that the genetic constitution of the population changed over time, as the individuals with a genetic capacity for greater thermal tolerance out-reproduced those less able to cope with the higher temperatures, Dallinger's increase in thermal tolerance in microbes is a classic case of microevolution. In contrast, the study of macroevolution focuses on changes in biodiversity over time, space and lineages, describing and explaining changes in the representation of lineages in the biota. Macroevolution has sometimes been considered a controversial topic, because it was considered by some to represent a challenge to the Darwinian hypothesis that the large scale differences in species found in different times and places are the result of the accumulation of many small genetic changes in populations. When I was an undergraduate we were discouraged from using the word "macroevolution" as it was thought to imply that there were non-Darwinian mechanisms shaping diversity that did not originate in microevolutionary processes (for background to this debate see Sterelny, 2007; Turner, 2011). Some researchers feel that observed patterns of biodiversity in space and time cannot be fully explained in terms of microevolutionary processes and must therefore call upon special macroevolutionary phenomena (e.g. Butterfield, 2007; Carroll, 2000; Erwin, 2000; Gould, 2002). However, these days macroevolution is an entirely respectable way to describe evolutionary studies that focus on patterns of representation of lineages, rather than on changes on genetic variants within single species, irrespective of the ultimate cause of those patterns (e.g. Goldberg, Roy, Lande, & Jablonski, 2005; Levinton, 2001; Nee, 2006; Purvis, 1996). So, in common with many biologists, when I use the term macroevolution I am describing observations about the distribution of biodiversity across large spatial, temporal and biological scales, regardless of the mechanisms that created the patterns of interest.

While the biological patterns under study differ between macroevolution and microevolution, most biologists work under the assumption that these patterns are all generated by the same basic processes: that is, that macroevolutionary patterns are generated by microevolutionary mechanisms acting over long periods of time. In practice, the timescales involved in macroevolutionary change put it well beyond the reach of direct observation or experimentation. Changes in biodiversity over such long timescales are generally not open to manipulation. Even the longest running evolutionary experiments, encompassing tens of thousands of generations of bacteria growing in a laboratory, illustrate phenomena of population divergence but do not generate biodiversity to the degree normally considered under macroevolutionary phenomena (Barrick et al., 2009). The practical upshot of this is that macroevolution is not studied as it happens, but after the fact, by observing the results of naturally acting processes, not by manipulating them directly.

As someone interested in macroevolution, I never perform classic, manipulative experiments. Yet in common with experimental biologists, my aim is to uncover causal relationships, by using hypotheses to generate predictions which are then compared to observation, through careful attention to experimental design and statistical analysis of my data. This view of a scientific test as a comparison of hypothesis predictions to observations can be applied to experimentation, observations, modelling and comparisons, such that we can test a scientific idea by sitting in a bird hide recording behaviour under different naturally occurring circumstances, or by comparing fossils from different time periods, or by

using a computer program to simulate the diversification of species under different models of speciation.

Here, I am using "prediction" in the informal sense of using what you know to make an informed guess about something you don't know. In the case of macroevolution, we are not usually in the business of making forward predictions about future events that are yet to happen. We might find it useful in some cases to make future prediction—for example which kinds of species are most likely to go extinct (e.g. Cardillo, Mace, Gittleman, & Purvis, 2006)—but it will rarely be the path to usefully discriminating macroevolutionary hypotheses. Instead, the word "prediction" is often used to refer to the use of prior knowledge to identify the most likely outcome, a process that is agnostic with respect to the timing of the outcome. In other words, a prediction is a statement about what is likely to happen if a particular set of condition is realized, given a particular hypothesis (Cleland, 2002), and it can just as well apply to what did happen in the past when a particular set of conditions occurred as it does to future events brought about by experimental manipulation.

There are two points that I would like to emphasize in this paper. One is that comparative studies, or "natural experiments", do not need to be seen as poor cousins to classical manipulative experiments, nor as imperfect attempts to mimic laboratory experiments. In fact, laboratory, field and comparative tests often employ similar design and analytical frameworks, and generally have the same basic goal of seeking relevant observations that allow discrimination of alternative causal hypotheses (Jeffares, 2008; Morgan, 2013; Okasha, 2011). Indeed, comparative tests or field observations can share not only the strengths of manipulative experiments (e.g. replication, ability to isolate variables of interest) but also some of the weaknesses (e.g. lack of transparency of causal mechanisms, difficulty in controlling covarying factors).

The second main point I would like to illustrate is that, in common with experimental studies, most comparative macroevolutionary studies do not provide a definitive test of a hypothesis. The heroic stories told of science usually focus on world-shaking discoveries (hence the obsession with Nobel laureates) or elegantly decisive "killer tests" that put competing ideas permanently to rest. While there is an entirely understandable tendency to focus on the rather more captivating examples where exciting new discoveries provide definitive answers to big questions, much of the progress is actually made by a more pedestrian accumulation of corroborating evidence from a range of investigations, weighed against case studies where a particular explanation can be rejected as less satisfying than an alternative (Currie, 2014; Stanford, 2011). Each study conducted adds grains to the balance in which hypotheses are weighed. This process of circling round a hypothesis by gathering evidence for and against a particular explanation using a collection of independent tests is not so different from classical experimental science, where the results of well-designed and precisely-executed manipulative experiments are often not as clear cut as might have been hoped.

Take the example of two high profile studies that aimed to test the hypothesis that caloric restriction increases lifespan (Sinclair, 2005). Two independent long-term manipulative experiments were carried out over several decades to discover whether restricting calorie consumption resulted in extended lifespan in primates, conducted by the National Institute for Aging (NIA) and Wisconsin National Primate Research Centre (WNPRC). Although each experiment was designed to be a definitive test of the hypothesis, they came to opposite conclusions: while both reported health benefits of calorie restriction, the WNPRC found that calorie restriction resulted in a 30% increase in lifespan (Colman, et al., 2009), but the NIA found no significant increase in lifespan in calorie restricted monkeys (Mattison, et al., 2012). In addition to

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