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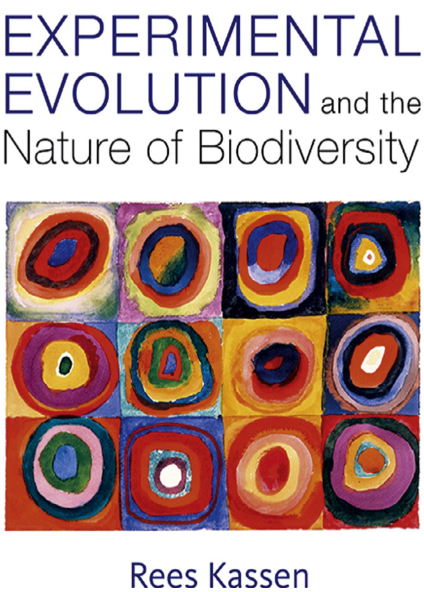
Book Review

Can Test-Tube Evolution Explain Biodiversity?

Tadeusz J. Kawecki[1,*]



What is the distribution of the fitness effects of alleles mediating adaptation to a novel environment? How is the evolution of niche breadth affected by environmental variability? How important are antagonistic pleiotropy and epistasis in diversification of lineages? How are rates of diversification affected by ecological interactions? Scientific literature is replete with theories addressing these fundamental questions. However, empirical support for these theories with data from nature is often less than satisfactory, not least because the evolutionary processes that shaped a taxon usually have to be inferred from a single snapshot of its evolutionary history. Enter experimental evolution, which permits direct replicated tests of predictions under controlled conditions [1]. Rees Kassen's *Experimental Evolution and the Nature of Biodiversity* testifies to the power of experimental evolution in microbial systems to address such questions and foster the development of a general theory of evolutionary adaptation and diversification.

The book is structured by theory. Successive chapters introduce briefly the assumptions, logic, and predictions concerning different aspects of adaptation and diversification. Kassen does an excellent job introducing the theory at an intuitive level. This comes at a cost; the theory is often simplified, the diversity of assumptions and predictions are glossed over, and only a few and not always the most relevant theory papers are cited. However, a real strength of the book is the thorough review of relevant results from microbial experimental evolution, summarized in extensive tables and correlation plots. Although the book stops short of formal meta-analysis, the evidence gathered provides a rather convincing support for some predictions; for example, that the rate with which successive alleles are substituted during adaptation to a novel environment decreases with time, or that diversification is hindered by the presence of competitors. Questions that need more data to be resolved are clearly identified. The focus on general models of adaptation leaves out some more specific topics, such as the evolution of parasite virulence, on which there is both rich theoretical work and a substantial body of data from microbial evolution experiments [2]. However, within its defined scope, *Experimental Evolution and the Nature of Biodiversity* is not only an authoritative review of the evidence, but also a great introduction for nonspecialists to both experimental evolution and the theories of adaptation and diversification.

Although the evidence reviewed in the book is limited to microbial experiments, Kassen's explicit motivation is to understand the nature of biodiversity beyond laboratory and beyond microbes. Jacques Monod famously stated that what is true for *Escherichia coli* is true for an elephant; ironically, his discovery of operons as a major feature of bacterial genome organization turned out not to extrapolate to eukaryotes. Despite carefully discussing limitations and caveats, Kassen might also be too optimistic about the extent to which the results from microbial experimental evolution can be extrapolated to sexual multicellular organisms. First, he espouses the view that speciation in 'macrobes' is usually initiated by ecologically driven diversifying selection; he plays down the cohesive force of sexual reproduction, implying that reproductive isolation evolves almost as a necessary consequence of the diversifying selection. While such 'ecological speciation' does seem to occur [3], the jury is still out as to its importance in generating biodiversity of plants and animals. The alternative view is that reproductive isolation in multicellular sexuals usually arises through accumulation of genetic incompatibilities or through divergence of mate recognition systems by sexual selection, independently of ecological adaptation [4,5]. Thus, ecological diversification may be a consequence rather than the cause of speciation. The data reviewed in *Experimental Evolution and the Nature of Biodiversity* cannot throw much light on this controversy, and even microbes that engage in occasional sex (e.g., yeast or *Chlamydomonas*) are not an ideal model system because they lack the extreme asymmetry in gamete size (or investment in offspring) that is the main driver of sexual selection in plants and animals [6]. Second, I am not convinced that the predominance of protein sequence over *cis*-regulatory changes in microbial evolution experiments helps to resolve the controversy about their relative contribution to diversification of

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animals and plants [7]. The complex regulatory mechanisms that orchestrate the development and cell differentiation of multicellular organisms arguably offer a broader potential target for evolution. Furthermore, adaptation in plants and animals typically involves changes in morphology, physiology, or behavior, which are mediated by specific cells and organs rather than by changes in biochemistry of all cells. This leaves more opportunity for evolution to tweak regulatory mechanisms in cell- or tissue-specific way.

However, a central message of this book does fully extrapolate beyond microbes: the genetic architecture of adaptive traits does matter for the evolution biodiversity. Thus, a general theory of diversification called for in the final chapter will require a synthesis of ecology and genetics of adaptation (and, for sexual organisms, of reproductive isolation [8]). Such a synthesis is easier in microbes, but this enjoyable book from an expert author motivates one to attempt it in other organisms.

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[1]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

*Correspondence: tadeusz.kawecki@unil.ch (T. Kawecki).

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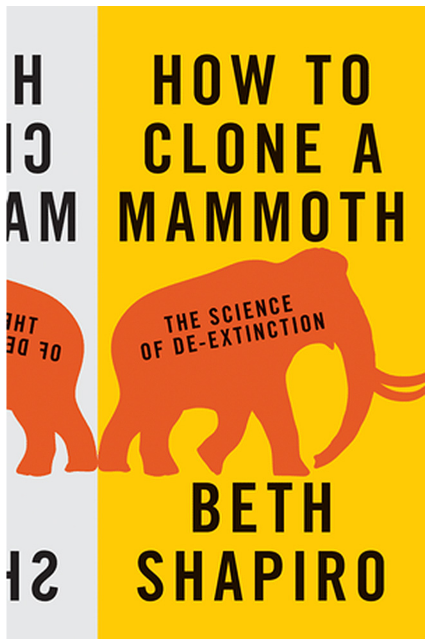
Book Review

De-extinction: Reframing the Possible

Philip J. Seddon[1,*]



I once found myself gazing at a forlorn exhibit: a nondescript stuffed pigeon – the remains of Martha, a passenger pigeon and the last member of a once hyperabundant species rendered extinct with her death in 1914. I am reminded of other last survivors, such as Lonesome George the giant tortoise, Richard Henry Kakapo, and Celia the Pyrenean ibex. Two things occur to me. First, if you are a member of an endangered species and someone names you, watch out; going on past records, your kind's days are numbered. Second, there is a sense of frustration and sadness at the loss of any species. Perhaps naturally, then, we imagine the return of lost species: 'if only you could see a live dodo, or imagine what a giant sloth must have looked like, sounded like, smelled like!'

A pickled pup became an unlikely poster child for early ambitions to revive lost species when, in 1999, the Australian National Museum embarked on a high-profile project to clone the thylacine – the Tasmanian wolf – that faded away as researchers came up against the technical challenges of deciphering old DNA [1]. Things have changed and there is now a productive research discipline that does just that: painstakingly reading fragments of DNA from museums, permafrost, and midden sites. Beth Shapiro explains how this can be done as she seeks to separate science from science fiction in her alluringly titled book *How to Clone a Mammoth*. Reading ancient DNA has been likened to reading an old book left out in the rain, where pages have been lost or retain only a word or a few letters. DNA is a fragile molecule but is a book worth reading if we can, containing the secrets of millions of years of evolution. Shapiro has been reading some very old books indeed, up to 700 000 years old and telling tales of ancient horses, giant bears, and saber-toothed cats.

In her book Shapiro charts advances in the ability to read ancient DNA in parallel with improvements in cloning technology and the rise of precise and efficient genome editing techniques such as CRISPR. These have raised all sorts of exciting and frightening new possibilities, perhaps few so engaging of the public imagination as 'de-extinction', a clunky and misleading term perhaps, but one that captures a sense of the wonder of the possible. De-extinction burst into public awareness in 2013 with a workshop, a series of TEDx talks, and a cover article in *National Geographic* [2]. Shapiro was part of this de-extinction launch, offering one of the more skeptical viewpoints but nevertheless attracting what amounted to hate mail from some of those who feared that de-extinction efforts might cause further declines in biodiversity should limited conservation funds be channeled into a handful of 'charismatic necrofauna' (Alex Steffen in [3]), or if the public loses a sense of urgency as the message 'extinction is forever' becomes watered down, or