Understanding adaptation and diversification: insights from the study of microbial experimental evolution.

Britt Koskella[1,2]

[1] BioSciences, University of Exeter, Penryn Campus, Tremough, Cornwall, TR10 9EZ, UK
[2] B.L.Koskella@Exeter.ac.uk

Review of: Kassen, R. 2014. *Experimental Evolution and the Nature of Biodiversity.* Roberts and Company Publishers. 288 pp. ISBN: 9781936221462; $36.00 PB.

Explaining the generation and maintenance of biodiversity is a central aim of evolutionary biology. This requires the integration of studies focused on explaining within-population diversity through to the organization of biodiversity at the ecosystem level. The combination of such comparative studies in nature with those employing experimental evolution in the laboratory is also valuable: the former helps build and test predictions for what processes might be driving patterns of biodiversity, while the latter can confirm whether such processes are capable of doing so in the absence of other biotic and abiotic factors. The recent increase in experimental evolution studies focusing on microbial populations has offered a number of key insights into the evolutionary mechanisms of adaptation and diversification relating to microbial organisms specifically, as well as into those mechanisms that are likely to generalize to non-microbial species.

In his new book on experimental evolution, Rees Kassen elegantly explores the empirical support for long-standing theories on adaptation and biodiversity that comes from both early and contemporary studies of experimental evolution. Each chapter begins with a short vignette that increases the readability and accessibility of the work. These stories provide broader context for each topic, beginning with the dawn of microbial experimental evolution and expanding to well-known contemporary systems such as Rich Lenski's over 61,000 generation experiment on *Escherichia coli* (Wiser et al. 2013) and more applied systems such as the diversification of *Pseudomonas aeruginosa* in the lungs of human cystic fibrosis sufferers (Smith et al. 2006). Kassen's discussion moves smoothly from population-level variation to lineage splitting to rates of speciation in order to achieve his stated goal of linking the microevolutionary process of adaptation to more macroevolutionary patterns of diversification. Taking full advantage of the clarity with which specific mechanisms and outcomes can be tested in the relatively simple and modifiable environment of a test tube, Kassen explores ideas such as the importance of spatial and temporal environmental variation, the repeatability of evolution, and the relationship between available niche space and diversification in both an intuitive and rigorous fashion. Each chapter concludes with a succinct set of conclusions and future directions that not only act as useful recaps of topics covered, but that would also help structure discussion in any reading group or journal club covering the book.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/evo.12564.

The major strength of Kassen's work is the keen attention to theory throughout, including discussion of the differences among empirical studies with regard to theoretical assumptions being met or violated. This focus on theoretical predictions allows for an interpretation of experimental results that is easy to apply to non-microbial organisms, with the necessary caveats in place. The first few chapters, for example, offer a comprehensive primer on mutational fitness effects (contrasting Fisher's geometric model with Gillespie's mutational landscape model), the fate of new mutations as a function of population dynamics, and the importance of how fitness is measured during experimental evolution. Later chapters explore the ecological theory of diversification and introduce theoretical work examining the genetics and genomics of diversification, such as the PEAD(R) model of potentiation, exaptation, amplification, divergence and reproductive isolation. In each case, evidence from microbial experimental evolution in support of or against theoretical predictions is discussed. The studies covered are not comprehensive, as can be seen from the relatively short citation list at the end of the book, but rather are offered as detailed examples of the power of experimental evolution and the type of data that can be obtained. For added depth of understanding, Kassen collates a large amount of empirical data into useful tables and figures, each of which could well make up a nice review article. For example, data from across 10 microbial experiments is used to demonstrate the preponderance of trade-offs observed as populations adapt to one environment and realize decreased fitness in another, and data from whole genome sequencing across 27 studies on fungi, bacteria, and viruses is used to highlight the decreasing rate of substitution commonly observed over the course of experimental evolution. These tables emphasize both the variation among systems in key traits relating to adaptive potential, and also highlight the general principles that are beginning to emerge across systems.

The key weakness of the book is related to its strength. Despite the generality of the title, Kassen's exploration does not extend much beyond microbial systems, which may be a disappointment to some readers given the wealth of experimental evolution studies from invertebrate systems such as flies, snails, crustaceans, and nematodes, as well as plants. However, covering the contribution of microbial experimental evolution is in itself an ambitious task, and even without the inclusion of non-microbial systems, the book feels both complete and accomplished. Of course, whether the assumption that "what is true for microbes in test tubes is equally true for all other living organisms" holds true depends on the nature of the question and predictions being tested. When exploring general evolutionary processes and testing broad mechanisms of evolutionary change, there is good reason to think results from *in vitro* microbial experiments *should* be broadly applicable. However, in cases where the processes driving diversity depend, for example, on reproductive isolation and/or recombination among populations there are clear reasons to be suspicious. Although microbial species often engage in a form of recombination in which genes are horizontally transmitted among unrelated individuals (Ochman et al. 2000), the impact of such genetic exchange is likely to have wholesale differences from that resulting from sexual recombination within and among populations. Furthermore, adaptation of asexual microbes in a test tube is nearly always limited by the rate of new mutations, which is in contrast to adaptation of sexual eukaryotes for which selection most often acts on standing genetic variation. Indeed, Kassen revisits the question of generalizability throughout the book, and even in the final chapter qualifies the conclusions in light of the key differences among primarily asexual microbes and sexual organisms.

Overall, Kassen does an excellent job of gathering evidence from a number of microbial systems and fields to build a unified argument for the connection between adaptation and diversification. Given its depth, unique synthesis of studies to date, and identification of open questions, this book will act as a great primer for students or researchers moving into the field of experimental evolution, but will equally serve as a thought-provoking read for those already embedded in the field.

Ochman, H., Lawrence, J. G., & Groisman, E. A. (2000). Lateral gene transfer and the nature of bacterial innovation. *Nature*, *405*(6784), 299-304.

Smith, E. E., Buckley, D. G., Wu, Z., Saenphimmachak, C., Hoffman, L. R., D'Argenio, D. A., ... & Olson, M. V. (2006). Genetic adaptation by Pseudomonas aeruginosa to the airways of cystic fibrosis patients. *Proceedings of the National Academy of Sciences*, *103*(22), 8487-8492.

Wiser, M. J., Ribeck, N., & Lenski, R. E. (2013). Long-term dynamics of adaptation in asexual populations. *Science*, *342*(6164), 1364-1367.