

Microbial evolution in action

Richard E. Lenski

In his introduction to this issue on microbial evolution, Richard Lenski describes his own research into *E. coli* populations and puts the other articles into context.

Most of us first encountered evolution as children, when we saw the fossil remains of dinosaurs and other extinct organisms in museums. As biologists, we also see the grand sweep of evolution recorded in the genomes of living organisms and, as microbiologists, we see on-going evolution in the emergence of microbes resistant to antimicrobial agents. Until recently, few viewed evolution as an experimental science. This is now changing as microbes are increasingly used in designed experiments to test various hypotheses about evolutionary dynamics, patterns and mechanisms.

For decades, some microbes served as model organisms in genetics and molecular biology. The same advantages – ease of culture, rapid generations and large populations – that served those fields also make micro-organisms ideally suited to experimental evolution. The advances in those fields, from technical approaches to whole-genome sequences, provide a powerful toolkit and a wealth of knowledge for analysing and interpreting results of evolution experiments with microbes. Many evolutionary questions are being addressed: the dynamics of adaptation by natural selection, the genetic changes underpinning that adaptation, tradeoffs between different aspects of performance, the specificity of adaptation with respect to environmental variables, the causes and consequences of hypermutability, the effects of population size, the maintenance of genetic diversity, conflict and cooperation in social interactions, effects of sexual versus asexual reproduction and co-evolution of hosts and parasites.

Evolution experiments with microbes are often quite simple, at least in concept. Populations start from an ancestral strain and are propagated in defined environments for many generations. The ancestor is frozen away, as are samples taken from the evolving populations at various generations. Later, ancestral and derived types can be revived and compared to determine what phenotypic changes occurred and to identify the genetic bases of those changes. One can even perform competitions between the ancestral and descendant types to measure the net change in Darwinian fitness that occurred during an experiment. (In human terms, it is as though we could bring back fossil hominids – not just their bones or bits of DNA, but the living beings – and challenge them to some competition – say, football or chess – to test whether and how much we have improved on our distant ancestors.) A genetic marker is often introduced to distinguish more readily the ancestral and evolved competitors. It is important to realize that the relative fitness of any two types depends on the environment, so the finding that a population has become

more fit than its ancestor under one set of conditions does not imply that it would be more fit elsewhere.

Some years ago, I began a long-term experiment in which 12 populations of *Escherichia coli* began from the same ancestral strain and have evolved in identical, defined environments for more than 20,000 bacterial generations (see Fig. 1). My two main objectives were to examine the reproducibility of evolution and to explore the coupling between phenotypic and genomic changes. In short, all the populations have become much more fit in the glucose-limited environment in which they evolved; at the end of 20,000 generations they grow about 75% faster than the ancestor when they compete head-to-head for glucose. There is much work still to be done on the genetic front, but one exciting result has been that global gene-expression profiles show strikingly similar evolution across replicate populations, yet sometimes these parallel changes involved mutations in different genes. I have reviewed our findings elsewhere.

In this issue, Paul Rainey reviews his experiments showing the rapid diversification of *Pseudomonas fluorescens* from a single genotype into several lineages adapted to different ecological niches that stably coexist even within a simple microcosm. He concludes that all microbiologists should realize that any experiment involving bacterial growth opens the door to evolutionary change. Of course, bacteria are not the only microbes that evolve: Peter Simmonds describes the tremendous speed with which viruses, especially RNA viruses, can evolve and adapt to different host environments. Frank Odds examines the troubling problem of antimicrobial resistance in *Candida*, an opportunistic fungal pathogen. We can take some comfort from evidence that fungal mutants suffer a physiological cost of evolved resistance, which reduces their fitness in the absence of antifungal compounds and thereby slows their spread.

Peter Williams describes rapid plasmid-mediated evolution of bacteria, which allows cells to degrade synthetic compounds that were never encountered in their prior evolutionary history. This article reminds us that many bacteria are friends, not foes, and evolution may sometimes work to our advantage in helping solve environmental problems. Finally, Lynn Margulis describes major evolutionary transitions in the history of life that emerged from endosymbiotic associations between micro-organisms. Remarkably, many of the hypothesized intermediate stages in these relationships can still be found among living microbes and subjected to investigation. Her perspective reminds those of us fascinated by studying evolution in action that our experiments are a mere drop in the deep ocean of evolutionary time.

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Further reading

Cooper, T.F., Rozen, D.E. & Lenski, R.E. (2003). Parallel changes in gene expression after 20,000 generations of evolution in *E. coli*. *Proc Natl Acad Sci USA* 100, 1072–1077.

Elena, S.F. & Lenski, R.E. (2003). Evolution experiments with micro-organisms: the dynamics and genetic bases of adaptation. *Nature Rev Gen* 4, 457–469.

Lenski, R.E. (2004). Phenotypic and genomic evolution during a 20,000-generation experiment with the bacterium *Escherichia coli*. *Plant Breed Rev* 24, 225–265.

BELOW:
Fig. 1. Twelve *E. coli* populations, evolving in and adapting to identical environments, provide a test of the repeatability of evolutionary dynamics and outcomes.

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