There's a speed limit to the pace of evolution, biologists say

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Researchers at the University of Pennsylvania have developed a theoretical model that informs the understanding of evolution and determines how quickly an organism will evolve using a catalogue of "evolutionary speed limits." The model provides quantitative predictions for the speed of evolution on various "fitness landscapes," the dynamic and varied conditions under which bacteria, viruses and even humans adapt.

A major conclusion of the work is that for some organisms, possibly including humans, continued evolution will not translate into ever-increasing fitness. Moreover, a population may accrue mutations at a constant rate -- a pattern long considered the hallmark of "neutral" or non-Darwinian evolution -- even when the mutations experience Darwinian selection.

While much is known about the qualitative aspects of evolutionary theory — that organisms mutate and these mutations are selected by the environment and are gradually absorbed by the entire population, very little is known about how, or how quickly, this is accomplished. Information on evolution between consecutive generations is hard to come by, and the lack of understanding has real-world implications. Public-health officials would have an easier time preparing targeted vaccinations, or combating drug resistance, if they understood the evolutionary speed limits on viruses and bacteria such as influenza and M. tuberculosis.

Penn researchers presented a theory of how the fitness of a population will increase over time, for a total of 14 types of underlying landscapes or "speed limits" that describe the consequences of available genetic mutations. These categories determine the speed and pattern of evolution, predicting how a population's overall fitness, and the number of accumulated beneficial mutations, are expected to increase over time.

Researchers compared the theory to the data from a two-decades study of *E. coli* to investigate how the bacterium evolves. Organisms of that simplicity and size reproduce more rapidly than larger species, providing 40,000 generations of data to study.

"We asked, quantitatively, how a population's fitness will increase over time as beneficial mutations accrue," said Joshua B. Plotkin, principal investigator and an assistant professor in the Department of Biology in Penn's School of Arts and Sciences. His research focuses on evolution at the molecular scale.

"This was an attempt to provide a theoretical framework for studying rates of molecular evolution," said first-author Sergey Kryazhimskiy, also of the Department of Biology. "We applied this theory to infer the underlying fitness landscape of bacteria, using data from a long-term bacterial experiment.".

In some theoretically conceivable landscapes, fitness levels are expected to increase exponentially forever because of an inexhaustible supply of beneficial mutations. But in more realistic landscapes the rate of adaptive substitutions (mutations that improve an organism's fitness) eventually lose steam, resulting in sub-linear fitness growth. In some of these landscapes, the fitness eventually levels out and the organism ceases to adapt, even though mutations may continue to accrue.

E. coli, for example, has been observed to increase its rate of cellular

division by roughly 40 percent during the course of 40,000 generations. Initially, the bacterial fitness increased rapidly, but eventually the fitness leveled out. These data have allowed the research team to infer that early mutations, while conferring large beneficial effects, also diminish the beneficial effects of subsequent mutations.

According to the study, a population's fitness and substitution trajectories —t he mutations acquired to achieve higher fitness — depend not on the full distribution of fitness effects of available mutations but rather on the expected fixation probability and the expected fitness increment of mutations. This mathematical observation greatly simplifies the possible trajectories of evolution into 14 distinct categories.

Researchers demonstrated that linear substitution trajectories that signify a constant rate of accruing mutations, long considered the hallmark of neutral evolution, can arise even when mutations are strongly beneficial. The results provide a basis for understanding the dynamics of adaptation and for inferring properties of an organism's fitness landscape from long-term experimental data. Applying these methods to data from bacterial experiments allowed the researchers to characterize the evolutionary relationships among beneficial mutations in the *E. coli* genome.

The study, appearing in the current issue of the journal *Proceedings of the National Academy of Sciences*, was performed by Plotkin and Kryazhimskiy along with Gašper Tkacik of the Department of Physics and Astronomy at Penn.

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