Highlight—Tracking Adaptation's Role: Do Larger Populations Evolve Faster?

Danielle Venton

Corresponding author: E-mail: danielle.venton@gmail.com.

Accepted: 6 April 2012

Imagine you have set a task for yourself: to breed a larger mouse. Taking evolution in hand, you select the biggest mice from your population each generation. After a few years, no surprise, you consistently have significantly larger mice.

What allowed this change to happen? The genetic diversity that makes evolution possible comes from two dominant sources: new, adaptive mutations and standing genetic variation. In our mouse experiment, the source of diversity would almost certainly be variation present in the population before we began tinkering. If, however, the selection lasted a long time, might novel, new mutations take a comparatively larger role? What role, if any, would the population's effective size play in shaping the evolutionary pathway?

Biologists have puzzled over such questions since population genetics took the stage in the 1930s. A study, seeking to address adaptation's role in evolution, was recently published in *Genome Biology and Evolution* (Gossmann et al. 2012). The study, which uses a new, favorably received statistical method, also uses data from species comparisons some researchers find questionable.

For many years, biologists have expected that species with greater reservoirs of genetic diversity, or larger effective population sizes, are faster at adapting to environmental change. "Although there's been some evidence of this in the past," says Adam Eyre-Walker, a paper coauthor, "we realized that the way people—including ourselves—were quantifying the rate of adaptive evolution was incorrect. It confounded two things, either of which could be affected by population size."

In the past, researchers have used the proportion of differences between species as a measure of how much change is attributable to adaptive evolution. "You're making a statement about two things simultaneously in looking at that statistic," says Eyre-Walker, a professor in the School of Life Sciences at the University of Sussex. If, for example, a scientist says 30% of the amino acid differences between two species are due to adaptive evolution, he or she is also making a statement about the other 70%—assuming that percentage has little to no effect on fitness. But, says Eyre-Walker, "it's actually a simple thing to just say something about the adaptive changes, without saying anything about the neutral ones. As a consequence, you're asking the question in the correct way."

In this work, to tease apart adaptive and neutral evolution, the team used nucleotide polymorphism and divergence data from 13 independent pairs of eukaryotic species. Prior to this point, researchers have generally found a correlation between the proportion of substitutions driven by positive selection and population size, though the question is not answered definitively. Using this new method of inquiry, the team finds the same thing—adaptive evolution matching population size.

Toni Gossmann, lead author and PhD student in Eyre-Walker's laboratory, thinks that the new way of measuring adaptive evolution will influence other researchers. "People tried to address the same question before," Gossmann writes, "however they looked at few species or looked at species comparisons—partly with inconclusive results. Consequently we were the first ones to do a meta analysis across multiple taxa from different phylogenetic groups."

Some of these comparisons, however, are unsatisfying for other researchers.

"I'm not overwhelmingly convinced by the evidence in their paper," says Brian Charlesworth of the Institute of Evolutionary Biology at the University of Edinburgh. Charlesworth, whose laboratory generated some of the data used in the Gossmann et al. paper, says important considerations have been left out.

According to one view of evolution, argued by theoreticians such as John Gillespie, the rate of protein sequence evolution is mainly driven by the rate that the environment changes. A reservoir of neutral mutations lies resting in the population. As surroundings change, some of these neutral mutations become favorable and spread.

Now, as a twist, Charlesworth also argues that favorable mutations likely get in each other's way if they appear in the same genomic region. If that region is unlikely to recombine, they have a hard time spreading through the population.

"There is quite a lot of evidence that regions of the genome where there is relatively little genetic recombination, are—in fact—missing out on adaptive evolution," Charlesworth says. "But this is not much discussed in the Gossmann et al. paper."

Also, some of the species compared in their analysis do not illustrate their point well, says Charlesworth. For example, the team uses the species *Drosophila miranda*, a species with low effective population size, for polymorphism data and compares it with *Drosophila affinis* for divergence data. They then estimate how much adaptive evolution is occurring, ascribing the difference to *D. miranda*.

"But actually," says Charlesworth, "*Drosophila miranda* is quite a long ways away from *Drosophila affinis*, so for all we know all that evolution is not going on in *Drosophila miranda* and its common ancestor with *Drosophila pseudoobscura.* It could be occurring between the common ancestor of *miranda* and *pseudoobscura* with *Drosophila affinis*."

Charlesworth also takes exception with several other comparisons used by the team. "I think they made a mistake. They're ignoring the fact that divergence from another species has nothing much to do with the effective population size that they're estimating for their species from which they're collecting the polymorphism data. [...] I think they've jumped the gun a bit and tried to do something that we can't really do at the moment. We don't have adequate data to make the comparisons."

Although the team stands behind their work, they concede that some of the criticisms may be justified. They are, they say, simply estimating current effective population size. Ideally, they would know the effective population size over the whole divergence history of two species. But, writes Eyre-Walker, they do not think their methods set up any systematic bias.

"It's actually surprising that there is a highly significant correlation despite the obvious shortcomings in the data," he writes. "However, we would like to emphasize that the analysis is only the second attempt to address what is an important question. We don't pretend that the analysis is perfect."

Literature Cited

Gossmann TI, Keightley PD, Eyre-Walker A. 2012. The effect of variation in the effective population size on the rate of adaptive molecular evolution in eukaryotes. Genome Biol Evol. doi:10.1093/gbe/evs027.

Associate editor: George Zhang