Evolutionary Rate

R E Lenski

doi: 10.1006/rwgn.2001.0432

Lenski, R E
Plant and Soil Science Building, Center for Microbial Ecology, Michigan State University, East Lansing, MI 48824-1325, USA

An evolutionary rate is used to describe the dynamics of change in a lineage across many generations. The changes of interest may be in the genome itself or in the phenotypic expression of underlying genetic events.

For example, one might be interested in the evolutionary rate during the domestication of corn (*Zea mays*) from its teosinte ancestor (*Z. parviglumis* or a related species). One would first need an estimate of the time since their divergence from a common ancestor, which in this case is approximately 7500 years ago based on archeological evidence from Mesoamerica (where corn was domesticated). The evolutionary rate of genetic change could be ascertained by comparing DNA sequences, ideally for several genes from a number of individuals of each species. To a first approximation, the rate of change can be expressed as the number of differences, per base pair sequenced, per year of divergence, where the time of divergence of two lineages is twice the time since their common ancestor. In practice, several issues may necessitate more complex analyses, such as the possibility that a single difference in DNA sequence may reflect multiple evolutionary changes; this particular effect is most pronounced when the sequences are highly divergent.

The evolutionary rate of phenotypic change could be obtained by comparing the values of one or more traits of interest, such as the number of seeds produced per ear or the concentration of oil in the seeds. These traits may depend on environmental influences, such as soil fertility, as well as on genetic changes; it is therefore important that the corn and teosinte plants be grown under the same conditions to isolate the effect of evolutionary changes in genotype from the direct effects of environment. The rate of change in a given phenotype could then be calculated as the difference in the average value of the trait in the two species, divided by twice the time of divergence. Note, however, that this calculation may give a misleading picture, as the common ancestor may not have had a trait value intermediate to the values in modern corn and teosinte. Indeed, it is likely in this case that the ancestor was much more like present-day teosinte, with most of the phenotypic change having occurred as a consequence of rapid evolution of corn under domestication.

Evolutionary rates differ quite substantially from one case to the next, and for a variety of reasons. In the broadest terms, evolutionary change at the genetic level depends on the interplay of several processes, including mutation, which produces new genetic variation, and natural selection, which influences the fate of any particular genetic variant. A few examples serve to illustrate two of the most important factors that influence rates of genetic evolution.

Replication and Repair

All cellular organisms have DNA as their hereditary material, but some viruses, including HIV (which causes AIDS) and influenza virus, use RNA instead. These RNA viruses undergo extremely rapid sequence evolution because RNA replication lacks the proofreading and repair processes that increase the fidelity of DNA replication. Even among the DNA-based bacteria, there exist mutants that are defective in DNA repair, and these 'mutators' should evolve much faster at the level of their DNA sequence.

Functional Constraints

A mutation may be deleterious, neutral, or beneficial in terms of its effect on an organism's reproductive success. Deleterious and neutral mutations are both very common, whereas beneficial mutations are much rarer and thus have less effect on variation in evolutionary rates at the genetic level. Because of the redundancy of the genetic code, some point mutations in protein-encoding genes (especially those at the third position in a codon) will not actually alter the amino acid sequence of the protein. Such synonymous mutations are therefore likely to be neutral. By contrast, nonsynonymous mutations cause a change from one amino acid to another, and such mutations often have deleterious consequences for the protein's function and, ultimately, the organism's performance. The extent to which nonsynonymous mutations are deleterious depends on their particular position within a gene as well as on the particular gene. Mutations that alter critical positions in a protein's structure are usually more harmful than those that affect a less crucial site. Evolutionary approaches can be used to identify conserved sequences, which in turn suggest potentially important features of protein structure and function. Among different genes, those that encode essential and highly constrained proteins can tolerate fewer mutations than those that encode less constrained proteins, which may accept a wider range of

mutations without compromising the organism's performance. For example, the rate of amino acid substitution in fibrinopeptides (proteins involved with blood-clotting) is more than 100 times faster than the corresponding rate in histones (proteins used to package DNA in eukaryotic chromosomes).

Neutral mutations serve as a sort of benchmark for understanding evolutionary rates, and they lead to the notion of a 'molecular clock' to describe genetic evolution. Population genetic theory shows that the expected evolutionary rate of genetic change for neutral mutations depends only on the underlying rate at which these mutations occur, and not on population size or natural selection. This simple result can be understood as follows. Let μ be the rate of neutral mutation and N be the population size, so that each generation $2N\mu$ new neutral mutations arise in a diploid population. Because they are neutral, each of these mutations has no greater or lesser chance of eventually being substituted in the population than any other of the $2N$ alleles present at a locus; in other words, a neutral mutation has a probability of $1/2N$ of becoming substituted. Given these considerations, the overall rate of substitution of neutral mutations is $2N\mu \times 1/2N = \mu$. In other words, the rate of genetic evolution would, in the case of neutral mutations, behave like a stochastic molecular clock which ticks at the rate μ.

Rates of phenotypic evolution are even more complex and variable. Whereas the balance between neutral and deleterious mutations is especially important for understanding rates of genetic evolution, neither of these classes is thought to play much role in phenotypic evolution – neutral mutations because they have no outward manifestation, and deleterious mutations because they will be eliminated by natural selection. Instead, phenotypic evolution depends on beneficial mutations, which are rare but extremely important because they provide raw material for organisms to adapt evolutionarily to their environments. Species that live in environments that hardly change over long periods of time typically show very slow rates of phenotypic evolution. Such organisms have presumably run out of ways to become better adapted to their environment, accounting for their phenotypic stasis. The horseshoe crab (*Limulus polyphemus*) is one such 'living fossil'; its outward appearance is very similar, although not identical, to fossils from more than 200 million years ago. At the other extreme, organisms in new environments often experience different selective agents and constraints from their ancestors, thus promoting rapid phenotypic evolution as they adapt genetically to their new environment. The conspicuous differences between domesticated plants and animals and their wild progenitors provide many examples of very rapid change. Another interesting example is the morphological divergence of Darwin's finches (*Geospiza* spp.) in the Galapagos Islands, where these birds experienced an environment different from their mainland ancestor. A critical factor in their rapid evolution was their release from competition with other species, which presented the island populations with the opportunity to fill ecological roles that would otherwise not have been available.

See also: **0533, 0840, 0881, 1161, 1615**