Finding Fitness: Adventures in Evolution
Sample Author sampleauthor@fit.edu

Introduction

~~Survival of the fittest. It has been the trademark slogan for evolution ever since Darwin founded the field, and the phrase has been used to promote everything from eugenics to reality-based television shows. Because of its common use in popular culture, survival of the fittest is also widely misunderstood. To gain an understanding of this slogan, we must first seek to define the key terms survival and fitness.~~

~~The term survival is fairly straightforward. In this context, survival denotes just how long an organism lives, but whether it lives to reproduce. This leads the crucial point that evolution applies only to those organisms that are able to reproduce. That means that no matter how well an organism carries out other life activities, it does not survive unless it produces offspring. For example, mules may be able to pull heavy loads better than other animals, but since they are sterile, they are non-survivors in the game of evolution.~~

~~Unlike survival, fitness is a very difficult term to define. We know that fitness describes an organism's ability to carry on life's activities, but a more precise definition seems elusive. Let's begin to investigate this complex notion by studying the simplest possible systems: populations of asexual organisms. In this realm, the notion of fitness may be reduced to "the ability of an organism to propagate its genetic material." In all Earthly biochemical life, genetic material comes in the form of DNA or RNA, but as evolution would presumably occur in the same way in alien life, we use the more general phrase. This definition of fitness yields two subtle but critical implications. First of all, it implies that fitness cannot be measured instantaneously. That is, an organism's fitness cannot be determined just by plucking it out of a population and performing some measurements on it. In order to determine the ability to propagate genetic material, we must examine the long-term success of the lineage that is founded by the given organism. The success of the lineage can usually only be determined after many generations of reproduction, long after the original organism has died. The second implication is that fitness is dependent on the environment. All organisms adapt to certain environments, and for every organism there exist environments in which it flourishes and environments in which it perishes. A splendid example of this is in the finches of the Galapagos, first described by Darwin himself (see Figure 4). Each species of finch is adapted to a very specific niche and environment. Although they survive well in their native habitats, they would probably be poorly equipped to deal with other environments. Thus, the idea of fitness only makes sense with respect to specific contexts.~~<u>Rewritten previously</u>

Figure 1
[insert figure 1.jpg] Darwin's Finches. The finches native to the Galapagos Islands have evolved to live in a variety of environments and eat a variety of foods.

Source: http://www.lclark.edu/˜seavey/darwinsfinches.htm.

About Quasispecies

Although the term fitness has now been defined, the concept remains very abstract. What we'd really like to know is what factors affect fitness and how we can measure such factors. Just brainstorming, we can think of numerous factors that affect an organism's fitness. For example, an organism's size, ability to gather food, and ability to escape predators would all affect its fitness. In fact, practically all life processes affect fitness in some way. This makes fitness a ~~horribly~~ complex function of many parameters that is essentially impossible to quantify. Fortunately, one value does seem to encompass all of these components: replication rate. Replication rate is the rate at which an organism produces offspring (i.e. number of offspring per unit time). So, by definition it should be nearly synonymous with fitness, right? Many members of the evolutionary biology establishment believe so, and fitness has traditionally been equated with replication rate.

However, some biologists, believe that fitness is not so simple. Eigen (see Eigen, 1971) developed a model called the quasispecies model. The theory introduces another component of fitness: robustness. While replication rate is an ~~fairly~~ obvious factor in fitness, robustness is subtler.

To understand robustness, let us revisit one of the implications of the definition for fitness: fitness is determined by the long-term success of an organism's descendants. In asexual species, organisms reproduce by making copies of all of their genetic material and then splitting into two daughter organisms. However, the offspring are not necessarily exact copies of the ancestor, for there is some finite probability of mutation in all real environments.

All species have a genome, the set of all possible genes any member of the species may display. Furthermore, the genotype space of a species is the mathematical space of all possible combinations of the genes in a genome. The quasispecies model is based on the fact that only a small fraction of all possible organisms in genotype space are viable (able to reproduce). The viable organisms usually occur in clusters of highly similar organisms called quasispecies. Quasispecies usually have one peak consisting of organisms with high replication rates, and the replication rate of organisms not on the peak decreases with increased number of mutational steps away from the peak organisms. Robustness is a measure of how quickly the replication rate decreases as a function of distance from the peak organism. The less quickly replication rate declines, the more robust the cloud is. Graphically, more robust organisms reside in quasispecies that are fat and round and less robust organisms reside in quasispecies that are tall and skinny. Two examples of the replication rate peaks of quasispecies are shown in Figure 2.

Figure 2

[Insert figure2.ps]
Caption: Fitness peaks of two quasispecies. Here, quasispecies A has a higher peak than quasispecies B, but its slope is much steeper. This means that while the peak genotypes of quasispecies A replicate faster than the peak genotypes of peak B, quasispecies A is less robust.

The quasispecies model predicts that in environments with low mutation rates, where nearly all offspring are exact copies of the ancestor, the replication rate of the original ancestor is the dominant factor in fitness. However, in environments with high mutations rates, more offspring are mutants of the ancestor, so the replication rates of the ancestor's quasispecies—and hence the ancestor's robustness—becomes important. Phenomena such as high-energy radiation and reactive chemicals can cause high mutation rates in natural environments.

Now we have a solid framework of precise definitions and two theories for fitness. One states that fitness depends only on replication rate. The other states that fitness depends on replication rate and robustness.

Although the nature of fitness is complex and subtle, there is a very straightforward empirical way to determine the fitter of two organisms of the same species. Simply place the two organisms in an isolated environment, give them the resources to grow and reproduce, and see which lineage (the ancestors with a common ancestor) becomes most prevalent in the resulting population. One lineage is said to "win" a competition when its number in the population greatly exceeds that of the other lineage.

To test our two theories, we ran competitions between pairs of organisms with different replication rates and robustnesses. For ease of discussion, let ancestor A denote the organism with a high replication rate and lower robustness and ancestor B denote the organism with lower replication rate and higher robustness compared to ancestor A. Let the respective lineages spawns by ancestors A and B be similarly denoted. The relationships between the replication rates and robustnesses of A and B are qualitatively similar to those of the peak organisms shown in Figure 2.

Normally, these types of experiments would be extremely difficult to perform. With biochemical organisms, it is very difficult to control the environment and mutation rate enough to separate the effects of different phenomena on fitness. Moreover, the experiments themselves are painstaking and time-consuming. Thus, we conducted the competition experiments using digital organisms, which in ~~the~~ recent years have proven a valuable tool in experimental evolution.

Figure 3

[insert figure3.jpg]

Caption: Digital Life. This is a schematic diagram of a digital organism in a population. The colored grid on the upper right represents a population, with the different colors being different genotypes. One organism consists of a series of simple instructions, some examples of which are displayed above the heading “genome.” Each organism has its own virtual processor, three registers (places to store data), and stacks (places to store instructions to execute) with which it carries out its metabolism of logical operations.

Results

The experiments were conducted using a platform called Avida (available at http://dllab.caltech.edu/avida/), which propagates populations of self-replicating computer programs in a fixed-size population of 3600 organisms (see Figure 3). Each organism consisted of a sequence of machine instructions taken from a set of 28 possible ones, with the genomic length of an organism being the number of instructions in its program. These 28 instructions have a strong analogy to the 20 amino acids that make up DNA. The genomes of all viable organisms contained some set of instructions that coded for self-replication, an asexual process in which the genome of a parent was copied into daughter organisms with a fixed probability of mutation. For these experiments, the mutations resulted from the erroneous copying of instructions during reproduction (a random instruction from the set of possible ones is copied instead of the correct one). These ~~mutation~~mutations are similar to ones that occur in biological replication when DNA base pairs are mismatched. The long-term evolution of these organisms was driven by rewarding organisms for doing certain logical operations, referred to as tasks, in addition to being able to replicate. In this environment, time was the life-providing resource, so those organisms that performed the most tasks were allowed the most time in which to execute their code, thus increasing their replication rates.

Discussion

Note, according to the traditional view that replication rate is the only factor in fitness, the outcomes of these competition experiments should be fairly boring. That is, lineage A should win at all environmental mutation rates. The quasispecies model, however, predicts something quite different. At low mutation rates, ~~the~~ lineage A should win as expected. However, at higher and higher mutation rates, lineage B should become more and more prevalent in the population until at a critical mutation rate lineage B actually starts to win the ~~competitions~~competition.

Figure 4

[Insert figure4a.gif (a) figure4b.gif(b)]

Caption: Competitions. Figures (a) and (b) show snapshots of two of the competition experiments between the same two starting organisms at different mutation rates, with the mutation rate in (a) being ~~one third~~one-third that of (b). Members of the lineage with higher robustness are colored purple and blue, and members of the lineage with higher replication rate are colored yellow and green. The four snapshots of the two growing populations during a competition experiment illustrate the dominance of the lineage with higher replication rate at the lower mutation rate and the dominance of the lineage with higher robustness at the higher mutation rate, as predicted by the quasispecies model.

In fact, the predictions of the quasispecies model corresponded with the results observed. Competitions were run between a total of 18 pairs of organisms at a variety of mutation rates. The competition ~~were~~was run for a fixed number of generations. Figure 4 depicts snapshots of two populations growing at two different mutation rates, illustrating the dramatic effect of mutation rate on the ~~grown~~growth of the two lineages. In Figure 4 lineage A is colored in yellow/green and lineage B is colored in purple/blue. In Figure 4(a), the mutation rate is ~~one third~~one-third the mutation rate of the population in Figure 4(b). As shown in the figure, at the lower mutation rate, lineage A dominates the population at the end of the experiment. At the higher mutation rate, lineage B ~~become~~becomes much more populous than lineage A. The two beginning ancestors and the two environments ~~is~~are identical except for the mutation rate.

Results qualitatively similar to those depicted in Figure 4 were observed in 12 out of the 18 sets of experiments, and only one contradicted the quasispecies prediction. In the six experiments in which the quasispecies prediction was not directly verified, the differences between the two ancestors were relatively small and the results within the threshold of experimental error. These results implied that at higher mutation rates, the advantage gained by having more viable offspring outweighed the disadvantage of replicating more slowly. This gives the more robust organism more descendants overall, or in other words, a higher fitness. The outcome of these competitions is very strong evidence for the quasispecies model. According to the traditional model, lineage B should never win, and yet 12 out of 18 times it showed a clear victory at high mutation rates. This shows that true fitness encompasses not only replication rate, but also robustness. In addition, the results support the hypothesis that natural selection takes into account not only the properties of an individual, but also those of the organisms that are its close mutational neighbors when determining the long-term survival of a lineage.

Conclusions

As no previous experiments have been performed to test the quasispecies theory against the traditional theory, the outcome of this study ~~are~~is both novel and compelling. With such dramatic results, it would be very beneficial to perform similar experiments with biochemical organisms not only to verify the effects of mutation rate on fitness, but also to compare the evolutionary dynamics of digital and biochemical adaptive systems. An excellent biochemical species to use in these experiments is E. Coli bacteria, which are simple, asexual organisms that share many characteristics with digital organisms.

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