I never told Stu Kauffman this, but, when I set out to climb fitness peaks with him 20 years ago as his post-doc, I was a bit suspicious that we were over-simplifying things – at least as far as biological evolution was concerned. Biological evolution, after all, is a dynamical process, and there are many aspects of the dynamics that are not obvious from knowledge of the landscape alone. While my subsequent career has been in quantitative finance, I kept thinking about these caveats, even as I was working with those infamous sub-prime mortgage backed securities, the ones that caused the financial crisis.

And I wondered if we are making similar mistakes in evolutionary theory. The textbooks define the fitness of an organism as the expected number of reproduc-tively viable offspring in a single generation. This definition has the same veneer of exactitude, the same pretense of quantitative certainty that I often see in finance. In finance, we have a parallel to expected number of offspring, and that is expected return on an investment. However, investing has another dimension – entirely distinct from expected return – and that is risk. There is a big difference between an investment for which a 5% return is guaranteed, and an investment where, half the time, returns are 40%, but a 30% loss is equally likely! Yet both of these investments have the same expected return of 5%. Similarly, equating fitness with expected numbers of offspring equates steady population growth with a population growth/decline that could lead to either huge populations or extinction. In fact, a population that is equally likely to grow by 40% per year and shrink by 30% per year will, with cer-tainty, eventually become extinct, as is evident from the following:

After N generations, suppose we have population growth in $G$ of those genera-tions, and population shrinkage in $N - G$ of those generations. Suppose further that,
if the population grows by the factor \( g \) if it grows and \( s \) if it shrinks. Then the population will grow to \( g^G s^{N-G} \) individuals per individual in the starting population after \( N \) generations (Note that this latter quantity is a random variable because \( G \) is.).

What are the circumstances under which \( g^G s^{N-G} \) is smaller than one? Whatever they are, they are certainly the same as those under which \( G \ln g + N \ln s < 0 \). But, by the Strong Law of Large Numbers, \( G = p_G N + o(N) \) with probability 1 as \( N \to \infty \), where \( p_G \) is the probability that there is growth for a given generation. It follows that there will be extinction with probability 1 if

\[
p_G \ln \frac{g}{s} + \ln s < 0 \quad (20.1)
\]

(In the situation given above, \( p_G = \frac{1}{2}, g = 1.4, \) and \( s = 0.7, \) so \( p_G \ln \frac{g}{s} + \ln s \approx -0.0101, \) thus proving my claim above.).

Finance also teaches us that no man – or company, or organism – is an island. Companies have suppliers, customers, and competitors. Organisms have prey, predators, and ecological niches. A projection of corporate earnings that ignores the overall state of the economy and a calculation of “expected number of offspring” of a deer that ignores whether nearby hunters have bows and arrows or deer rifles are equally meaningless. Yet the above definition of fitness ignores the fact that coevolution can re-define the dynamics of evolutionary change to the point where fitness in a static environment is no longer relevant. Also refer to the discussions in the Chapters 10, 11 and 12 of this book.

Perhaps the most precise possible definition of fitness can be found in Eigen’s quasi-species theory [2, 3, 4]. Given the experimentally observed sequence specific replication of RNA macromolecules in vitro in the presence of appropriate RNA monomers and replication enzymes, fitness is simply the replication rate of a specific sequence. Yet, even in that simple case, the fittest (in the sense of fastest replicating) sequence was not the only one that survived. Instead, sequences that were likely to arise from copying errors of the rapid replicators were also found, even if these sequences were, themselves, not quite the best. In fact, depending on the details of the replication rates of all of the sequences involved, the sequence found in the highest concentration might not have the absolute fastest replication rate, but might, instead, be the likely beneficiary of copying errors from many other sequences with slightly faster replication rates but with fewer close mutants that also have fast replication rates.

In settings closer to what we would generally think of as biological, the concept of fitness is even more problematic. Almost every organism interacts with the rest of the biosphere as a prey species for some other organism or a predator of some other organism or both. Thus, the dynamics of that organism’s population growth and decline must also account for the population of its predator(s) and/or prey, necessarily coupling the dynamics of all species involved. Even the simplest form of this coupling, in which the growth/death rate of the first species is proportional to both its current population size and that of the prey/predator, is non-linear, in contrast with the linear growth rate implicit in any reasonable definition of fitness. So, not surprisingly, we find all of the behaviors – stability, limit cycles, and even chaos