Evolutionary Dynamics

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Week 06

Lecture 29

Hi everybody, welcome back. We are going to change gears now from the fitness landscape and discuss an extremely important facet of evolution. So far, what we have talked about is that natural selection drives evolution forward. Should a beneficial mutant arise in the population, natural selection is going to favor that beneficial mutant because it will have more progeny compared to an individual with lower fitness. As a result of that, as time progresses,

the more fit individual is going to produce more progeny and will outcompete the progeny of the less fit individuals. And as a result, the population structure will move toward the more fit individual, eventually leading to the extinction of the less fit individuals. In other words, graphically, this can be depicted as follows. Let us say we have a landscape like this. This is fitness.

And at t equal to 0, we have individuals of this particular genotype. Let us say this is AA. And these genotypes reproduce, and equalized reproduction usually leads to progeny that has an identical genotype to the parent. So if this reproduces, the progeny also has the same genotype, and so on and so forth. Rarely, a beneficial mutation will occur that increases fitness.

So let's say this is AT. And then we have one individual of this kind. In the view of evolution that we have been discussing, the following happens thereafter. This looks like this. AA, AT.

In the view of evolution that we have been discussing so far, what we've been saying at this individual, because it's higher in fitness as compared to the green individuals, is going to reproduce faster. As a result of which, the number of progeny that this individual have is going to be more than the number of progeny that a green individual has in a given amount of time. As a result, if I move forward in time, the population will look something like this. That here, the fraction of red individuals was 1 upon 7.

there were seven individuals in the population in all, one of which is red. So the red individual frequency is this. And as time goes forward, progeny of red are able to outcompete the progeny of green. As a result of this, the fraction of red individuals reaches three by seven in some time. And if we let this play a little more,

Eventually, this will lead to the following situation that we have with no green. So the fraction of red individuals is 7 by 7, which is simply equal to 1. And thereafter, we wait for a mutational event such as this to take place, such that one individual like this is going to be born, and so on and so forth. This model of evolution was also represented by the mathematical equations that we wrote, where we wrote the following: dx by dt was equal to x into r of a minus phi, and dy by dt was y into r of b minus phi, and in this case, a and b are the green individuals and the red individuals. And because, in this case, from the graph, we know that the fitness of red individuals, which is RB, is greater than the fitness of the green individuals, RA, and phi, if you remember, is the mean fitness of the population. RB is always going to be greater than phi. Hence, y will keep on increasing in the population, whereas x will keep on decreasing in the population. x and y, from our previous discussion, are the fractions of individuals in the population which are of type A and B.

$$\frac{dx}{dt} = r_A\, x\, (1 - \emptyset)$$

$$\frac{dy}{dt} = r_B\, y\, (1 - \emptyset)$$

This view of evolution tells us that evolution, as a process, is a very deterministic process. That once a beneficial mutation occurs, that beneficial mutation is driven by natural selection to outcompete the less fit individuals. And hence, we transition from one red individual to all red individuals. And then the process keeps on repeating itself in the next mutation, which is going to be, let us say, on the sequence space TT. And one of these individuals is going to pick up this mutation.

This sort of a view that we have been trying to we have been painting in this in our discussions is a very deterministic process. it doesn't quite tell us what is the role of chance in evolutionary processes. Also remember the quote that we had from the late paleontologist and evolutionary biologist Stephen Gould. There's an interesting reference for anybody who's interested called Wonderful Life. That Gould wrote in late 80s and it's a fantastic read.

He has a whole bunch of essays about evolution and life on the planet in general, which are a great joy to read for anybody interested. Remember that Gould said that if we rerun the tape of life, the phrase that he used was tape of life. If we rerun this on Earth for the last four and a half billion years, then would evolutionary process be deterministic enough such that beings like us are present on the planet or evolutionary processes are so noisy that the fate of this four and a half billion year experiment is going to be completely different in this other manifestation scenario. when we are alternatively running this type of life on this parallel earth for 4.5 billion years.

So this is a question of what if this is a discussion of what we have been doing is a discussion of deterministic process of evolution. How does chance come into being? And that is what we'll spend the next few videos discussing. And we'll realize, perhaps surprisingly, that how important chance is in dictating evolutionary processes. To begin with, let's start with the following example and I will describe this example and after that I would like all of you to take 30 seconds and think about a question that I will pose.

Imagine a chemostat. Its capacity is V. Inlet and outlet flows are small v naught. These are rates, and these are stirred. And at t equal to 0, the state of the

reactor looks like this. There are bacteria in it, and the same color indicates the same genotype, hence the same fitness. So, at t equal to 0, the reactor looks like this, except for the fact that there is one individual which is of a different genotype and hence a different fitness. If you look at these two genotypes, let us imagine that the fitness of this individual is 1.05. We saw from the E. coli evolution experiment that a typical fitness conferred by a beneficial mutation is of the order of 5%.

And to keep it at 5%, let us say that the ancestor's fitness is 1. So this scenario at t equal to zero represents the case where a beneficial mutation has just occurred in the population. And as a result of that, this blue individual has come into being. All the other individuals in this population are of the same fitness, one. If I'm talking about the population structure, let's say that the carrying capacity of this chemostat is N,

So there are N minus one individuals which are of this kind, and there is one individual which is of this kind. That's the scenario that we have. That's the picture of the chemostat that we are looking at at t equal to zero. If we give this process a sufficient amount of time—so, let's say, without being mathematically precise about it—let's say we give it sufficient time. The question that I have is that natural selection tells us this blue individual is fitter, and hence the reactor should reach the following state.

That the blue-type individuals should be N, and green-type individuals should be 0. So, the fraction of individuals of blue type, which was 1 upon N—1 is the number of blue-type individuals, N is the total number of individuals in the reactor, which is N minus 1 plus 1. So, the fraction of blue-type individuals was 1 upon N. By the time this sufficient time passed, the fraction of individuals of blue type became N upon N, which is just 1. And natural selection should drive this change, as we have come to understand it. The question that I have—that I would like you to think about for 30 seconds or so—is, let us give these two states a name.

Let us call this state A. Of the reactor as state A, and let us call this at a later time as state B. And the question that we should think about is, what is the probability that the reactor or chemostat reaches state B, given that state A has already happened—so this blue mutation has already occurred in the population. And the second thing that's given to us is that no new mutations occur thereafter. Realistically, new mutations will obviously take place because N is going to be a very large number for a microbial population.

And we see that errors are made every 1000th division. But for the purpose of this discussion, we will relax this assumption as we move forward in our discussions. But for the purpose of this question, we are going to assume that state A is already reached. As I look at the chemostat at this instance, state A is reached. There is a blue-type individual.

The rest are all green-type individuals. And I am asking, what is the probability that the chemostat reaches state B? Take 30 seconds. Obviously, this is probability, so the probability is going to be a number between 0 and 1. I would like all of you to take 30 seconds to decide, to sort of think about this question and think of a number between 0 and 1, which conveys your intuition about how this process is going to go forward.

So we'll wait for 30 seconds and then reconvene. So one possible answer that you could be thinking of is that the probability of going from A to B is simply 1, because this type of individual, this blue individual, has come into the population. We are given that the blue individual is fitter than the green individual. As a result, as time moves forward, the blue individual is going to start replacing the green individuals. It's going to have more progeny as compared to the green ones in a given amount of time.

And as a result of that, as this moves forward, this fraction of the population, which is the blue type, is going to increase, eventually going to one when there are only blue-type individuals left in the population. Hence, this is a very deterministic process that will happen in such a setting. However, that's not the case. And the reason for that is

Again, it would be a good exercise to pause the video and think of scenarios where this transition will not take place. And these are the two rules that are given to you: that state A has already been reached and that no new mutation will occur thereafter in the system. What should strike you is that the following scenario can happen. That you have this reactor. And this has blue individuals.

I'm sorry, there's only one blue individual. So we have this reactor, and there are green individuals in the reactor. And there is only one blue individual present in the population. And this is a continuous process. There is a continuous influx of V naught and a continuous outflux of V naught.

The capacity of the reactor is V. If natural selection was the only force acting, then it is correct to say that this transition would happen with probability one, that it's a deterministic force acting more fit individuals are going to replace the less fit individuals and hence this transition will take place. However, this process, the fate of this chemostat is dictated by natural selection, which is pushing the system in a direction where blue individuals take over, or chance events which make the system's response difficult to predict. And what might happen is that imagine in the current state this particular individual is close to exit and there is continuously V0 volume per time being withdrawn from the system at any given point in time.

If that is the case, then it is possible that this individual is removed from the system before it had even a chance to divide. If a blue individual gets washed away from the system, then our chemostat is left with only green individuals and the chance that this chemostat with only green individuals will transition to all blue is zero because the only blue individual in the system has been lost because of the exit stream. Now whether this individual will be lost or not is a matter of chance and that is what decides whether the system will go to this fate or it will go to this alternate fate where there are only green individuals present in the population. Let's imagine that this blue individual, if there is only one blue individual in the chemostat and it's washed away, the game is over.

We go to this all green state. However, let's imagine that it doesn't immediately get washed away. It gets some time in the reactor and it's able to produce, it's able to divide once. And now we have this scenario where there are two blue type individuals in the population. But even now, there is a chance that both these blue individuals are washed away from the population and the system goes to this state, all green state.

This chance of both these getting washed away before either one of them had a chance to divide is smaller as compared to when there was only one blue individual which could get washed away. The probability of one getting washed away is much higher as compared to probability of both of them being lost from the reactor. But there is still some chance that both might get lost and then you get to this all green state. And so on and so forth. The same logic will apply for 3 and 4 and so on and so forth.

And we should realize the more time passes and more the number of blue type individuals in the reactor, the difficult it is for all the blue type individuals to get washed away and chance to drive the system to this state where there are only green individuals in the population. it becomes increasingly harder for the system to move to all green and natural selection will then drive to this particular state. So what we see is that if this is the number of blue type individuals in the population, if there are very few then there is a good chance that chance will decide fate. But as the number of blue type individuals increases, let's say there are that many, now the role of chance has gone down and role of selection has gone up.

And if the number of blue type individuals is very large, which just means that chances roll decreases because imagine there are 50,000 blue type individuals in this reactor now. And chance that all 50,000 are going to get washed away before they even divide is really small. So the system will not likely go to the green state. Almost definitely the system will go to the blue state. So there is evolutionary fates are decided by this tussle between chance and selection events that are taking place.

And the relative strengths of chance and selection keep changing with time, depending on the precise state of the system. In the state when there is only one blue individual here, it's difficult to say, chance has a much greater role to play, and as a result, it's difficult to say what the final state of the system will be. But if I told you that starting out there are 50,000 blue-type individuals, then we can say with much greater certainty that blue is going to replace the green-type individuals in the population. So the relative strengths of chance and selection change with the composition of the population.

So going back to the question: if we start with one blue individual, what is the probability that the system reaches all blue? That's the probability that we will start to derive from the next video onward. And we are interested in studying the transition from one blue to all blue because whenever a beneficial mutation occurs in the population, it's only going to occur in one individual. By definition, a beneficial mutation will only occur during a division process in one individual. Hence, the beneficial mutant with higher fitness is going to arrive in a population of n where its own number is only one.

And hence, we are interested in studying the transition from one such individual to all such individuals. That is the transition we are interested in studying, and that is going to be true for any beneficial mutation that occurs in any population. It starts with only one individual carrying that mutation and may reach a stage where everybody is carrying it, as shown in the figure here. Alternatively, it could also happen that this beneficial mutation is lost due to chance, And the system returns to the state it was in prior to the occurrence of the mutation, that is, all green individuals.

And these numbers, when we calculate these probabilities in the next few videos, are somewhat surprising. At least they were surprising to me when I first studied this subject. And we'll start this discussion from the next video onwards. Thank you.