Evolutionary Dynamics
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Lecture 19

Hi, welcome back to the next video. Let's continue our discussion on the growth model in a chemostat where two species are interacting and competing with each other. So, this is where we left off. At the end of this analysis, we had the following equations: dx by dt is growing at a rate which is proportional. So, this is the growth term, which is new bacteria being added—new bacteria of A type. Being added because of growth.

As against this, this is the force that the A-type bacteria are being washed away by the exit stream. And while this term was relatively easy to write—that the growth or the addition of A-type individuals in the chemostat is going to be simply proportional to the growth rate of A-type individuals, which is RA, and also going to be proportional to how many A-type individuals are already there, which is X—this was relatively straightforward to write. But for the washing away term, we knew that this was going to be proportional to X because this is a continuous tank reactor and everything is well mixed. So if there are 90% A-type individuals in the chemostat and I take out a small volume V0 from this and examine what is going to be the A-type individuals in this volume that I have taken out, it is also going to be 90%. That is the property of a continuously stirred tank reactor, which is well mixed.

But what we did not know is what this quantity phi is. And because of the analysis that we did in the previous video, we know that phi is just the mean growth rate of the population at any given point in time. What we have to realize here is that phi—let us formally write this down—that phi is the mean growth rate of the population at any given point, and I say at any given point in time because while at a certain instant of time, when let's say X is 0.4 and Y is 0.6, phi is going to be RA times 0.4 plus RB times 0.6.

But let us say that RA is bigger than RB. So, as time moves forward, x has increased to 0.8 and y has reduced to 0.2. In that scenario, phi is just going to be equal to RA times 0.8 plus RB times 0.2. So, the value of phi has changed because the composition of the population has changed as we move forward in time. Another way to understand this would be that if we were to make a scale like this, let us say on a scale, we have RA and RB.

So, what we are saying is that B is more fit than A. And by more fit, we mean greater growth rate. Now, if I have a population, let's say I'm talking of different population structures. If I have a population structure which is 100% A, 0% B, Then the mean fitness of this is going to be RA times the fraction of individuals that are A, which is 1, plus RB times the fraction of individuals which are B, which is 0.

That's just equal to RA. So, the mean fitness of this population, let's call this population number 1. So, the mean fitness of population number 1 is going to be this point. On the other hand, if I have a population structure, let us not work in terms of percentages, let us work in terms of fractions. So, in this case, we are saying the fraction of A-type individuals is 1, the fraction of B-type individuals is 0, and hence the mean fitness is RA.

Growth rate of A into fraction of A type individuals plus growth rate of B into fraction of B type individuals, which in the case when fraction of A and B is one and zero respectively, will be simply equal to R A. And hence for this for population number one, the mean growth rate is represented by that point. Now, let us look at another case where let us call this case number 2 when fractions are 0.5 and 0.5. So, this is in this case the mean fitness is going to be RA times 0.5 plus RB times 0.5 which is just equal to RA by 2 plus RB by two, which can be written as RA plus RB divided by two. So this means this is the exact midpoint of RA and RB.

So for a population with this structure, mean fitness is just RA plus RB by two. So population number two has a mean here. And let's just do one more. which is 3. And let us say in this case, fraction of individuals of A type is 0.1, fraction of individuals of B type is 0.9.

In this case, the mean fitness is going to be RA times 0.1 plus RB times 0.9, which you should realize is much closer to B than to A. Because this combined number is 90% of B and only 10% of A. When it was 50% A, 50% B, it was right at the center. This is 90% of B. So this is going to be very close to B, but not quite equal to B. And this is where it will be. So depending on what the point we are trying to make is that depending on the structure of the population, depending on the structure of the population at any given point at any given point in time the mean fitness phi changes and that is the key idea that we have to remember.

In this case, it's clearly illustrated that these are three different populations with three different values of phi. So, again, let us go back to the equation that we were writing, and rewriting the equation, we have dx by dt was simply equal to Ra times x minus phi times x. Now, I can write this as Ra minus phi times x, and if I look at this a little closer, What I should note is that X is the fraction of individuals which are A type. Since this is the fraction of individuals, this is always going to be greater than zero. On the other hand, in this bracket, we have RA minus phi.

Phi, remember, is the mean fitness. So, what we are saying here is that in the case when RA, the fitness of A, is bigger than phi—so when A is fitter than the mean—let us write down: if A is fitter than the mean, In that case, this quantity rA minus phi is also greater than 0, which means dx by dt is equal to rA minus phi times x, where this quantity is greater than 0, this quantity is greater than 0, which implies dx by dt is greater than zero, which implies as time increases, X increases. And that is not surprising because X is the fraction of A-type individuals, and A-type individuals have a greater fitness than the mean; hence, they will continue to increase in their frequency until the point rA minus phi becomes less than zero. If rA minus phi is less than 0, then we have dx by dt is equal to a number which is less than 0 times x, which is a number greater than 0, which is a negative number into a positive number, resulting in a number less than 0.

So, dx by dt in that case is less than 0, which means that as time increases, X decreases. So we get a simple rule—we get a mathematical formula with which we can predict the quantities, the fraction of individuals of any particular genotype in a chemostat at any given point in time. But we also get an intuitive relationship. And the intuitive relationship tells me that as long as the fitness of A-type individuals is greater than the mean fitness, A will continue to increase in frequency.

It is only when the fitness of the A-type individual becomes less than that of the mean fitness that A will start to decrease in frequency. So we can extend that to any environment now with any number of species. That if in a chemostat with N different species, if the fitness of the ith species is greater than the mean fitness, its numbers will keep on increasing continuously. And if at any given point in time the fitness of the ith genotype, the ith species, becomes less than that of the mean fitness, then it will start to decrease. Let us formally write this: that now if we have N species in a chemostat,

let us call them species A, B, going all the way to N. Then at any given point in time, if fitness—and by fitness we are using growth rate as a proxy—if the fitness of the ith species is less than the mean fitness of all N, that implies that the ith species will decrease in frequency. On the other hand, if the fitness of the jth species is greater than the mean fitness, this implies that the jth species will increase in frequency. And it's this simple rule that we must keep in mind, although we also have an exact mathematical framework in which we can understand this phenomenon. But for our purposes, for the time being, we are interested in this qualitative understanding of when a particular species increases in number and when it starts decreasing in numbers.

So these are the three frameworks in which we will be looking at growth rates. And although we are done with them for now, as we discuss specific examples of what we have seen in evolutionary experiments in the lab, we will keep invoking one of these three models depending on the context we are discussing and understanding those results in the framework that these three models provide to us. For now, we want to understand one big limitation of what we have discussed. So what we said is that this chemostat, this chemostat is occupied by two different species, B and A. And as growth happens, B-type gives rise to B-type individuals, and A-type gives rise to A-type individuals.

These have growth rates associated with them, which is RA, which is a measure of fitness in the framework that we are using. The B-type individuals are growing at growth rate RB. And when a B-type individual divides, it gives rise to two B-type individuals, which also grow at growth rates RB and RB. And same for the case of A-type individuals, that when an A-type individual divides, it gives rise to two A-type individuals whose growth rates are RA and RA. This is a huge assumption that we made while deriving the results that we did for the chemostat just now.

However, we've already seen that bacterial populations are extremely large. As a result of that, whenever mutations, as a result of that, Because of these large population sizes and finite mutation rates, we have mutations occurring all the time. So every once in a while, we will have a progeny that is produced, which is carrying a mutation and whose growth rate as a result of that mutation is not RA, but in fact is RA dash. And RA dash is not equal to RA.

The framework that we have developed so far only allows us to look at where new mutations, new variants are not coming up. All the variation that we have analyzed so far was existing beforehand where A and B type individuals were existing in the chemostat already. Or in the second case that we discussed that A to N type individuals species were existing in the chemostat already. And we can comment on which individual increases in frequency and which individual decreases in frequency. But we very well know that when this chemostat is operating, new individuals are coming up, mutations are happening.

Newer forms of variants are also going to come up into the chemostat. So we're going to look at some of these ideas and what do they tell us? What do they tell us about how to think of these processes? So first idea is that fitness. In this context is being measured by growth rate.

This is an approximation and is only valid when I am selecting for fast growing bacteria. For instance, this is a chemostat. But suppose let's go back to the example of a batch culture. In a batch culture, if I have two species A and B, let's imagine that the first one grows like this. This is, let's say, species A.

And let's imagine that competing against it is this species B, starting from the same number, species B. So the question before me is that what is a more appropriate proxy for fitness? And that depends on what am I looking at? At what point in the growth curve am I looking at these numbers? So this is time and this is number. If I am comparing species A and B at around this time, where this one is growing exponentially, this one is also growing more or less exponentially.

If my comparison is at this point, then what I'm selecting for or what imparts greater fitness to one variant over the other is a high growth rate. So then, growth rate is the Growth rate is an appropriate measure of fitness. However, if the same comparison between the two species is being done at this point, then growth rate is the appropriate measure of fitness. And in this case, what I will end up saying is B is fitter than A.

However, if I'm comparing them here, then my comparison is a result of the growth that happened, the stationary phase that they stayed in, and the death phase that they stayed in for however long. As a result of all these three put together, what has resulted here is that species A is fitter than B. And because of that, growth rate is no longer an appropriate proxy for fitness because if we're simply looking at growth rates, then B is rising much more rapidly compared to A, and I would have said that B is fitter. In fact, when I make the comparison at this point, it's A which is fitter than B. So growth rate is not a good proxy for fitness. So these contexts have to be extremely carefully studied when we are defining fitness in different contexts.

For our purposes, for the time being, let's imagine that fitness is being defined by growth rate. So in the chemostat that we are looking at, In the chemostat that we are looking at, there are A and B type individuals. And let's imagine that we have a B-type individual which is growing at growth rate RB. So this is its fitness.

And post-division, it gives rise to two individuals. One of them carries a mutation. So one progeny grows at the parent's growth rate, RB, while the other grows at RB dash. Now, we know after having examined the molecular basis of mutations that this is likely just a nucleotide change. It could be an insertion, deletion, duplication, and so on.

As a result of whatever genetic basis this mutation has, the growth rate changes. This allows me to classify this mutation into two broad categories. The first one is called a beneficial mutation. This occurs when RB dash is greater than RB. The progeny resulting from this mutational event grows faster than the parent it originated from.

As a result, this is called a beneficial mutation because it provides some advantage to the progeny. In contrast, we could also have deleterious mutations. Here, RB dash is less than RB. This would result when the mutation causes something to function less effectively than in the parent. Consequently, this progeny grows slower compared to the parent it came from.

We shouldn't forget the third type of mutation that is also possible. that a mutation happened, but neutral mutation. That a mutation happened, however, that mutation had no effect on growth rate. So the difference between neutral mutation, this case, and this case, is that in this case, there was no mutation. the genotype of this individual and this individual are identical.

However, in the neutral mutation case, the genotype of this individual is carrying one mutation. It is just that in the environmental context in which growth is taking place, in this environmental context, this particular mutation has no effect on growth rate associated with the bacteria. So as these new variants are coming up in the chemostat, their mutational effects are going to be either beneficial, deleterious or neutral. Deleterious mutations are easy to think qualitatively as to regarding to what they would be their fate. We already have a large population of B type individuals which are growing at rate RB and

This individual which is growing at a rate less than RB is going to be outcompeted from the population. Outcompeted from the population. And this goes extinct. So we don't have to worry about deleterious mutations too much. Beneficial mutations obviously lead to rise to an individual which is growing faster than the parent population.

And its fate is an interesting problem that we will look at in two to three lectures or so. And neutral mutations behave phenotypically as though they are growing at the same rate. However, the underlying genotype associated with them has obviously changed. One thing we will discuss before we end this lecture is to consider a beneficial mutation. So we started with an individual, let's say this was RB, and then this individual divided. One of the progeny has a mutation growing at rate RB dash, and the other one doesn't have a mutation and is growing at RB.

At the same time, in the same chemostat, another B-type individual is growing at RB. It divided and picked up a mutation. And let us say this individual is Rb naught, and this is Rb. Both these mutational events are beneficial mutations. What that means in this context is that Rb dash is greater than Rb,

and RB0 is greater than RB. So, both these mutations are what we just described on the previous slide: beneficial mutations. However, Does that mean that all beneficial mutations are of the same kind? No.

Although they are both beneficial, the benefits that they confer can be different. Say it is different. And this The quantum of benefit that a mutation confers is called the selection coefficient of a mutation, the selection coefficient of a mutation. This is represented in evolutionary biology literature as a small 's,' and it's an extremely important variable in evolutionary biology that you will see referred to all the time.

Let's look at this one. So, let's call this mutation number one. So, for mutation number one, The selection coefficient of mutation number one is simply defined as RB dash minus RB divided by RB, which can also be written as RB dash divided by RB minus one. So, this is the fitness of the new individual divided by the fitness of the parent individual minus one.

And because we are saying that this was a beneficial mutation, the fitness of the new individual is obviously going to be greater than the fitness of the parent individual. Hence, this ratio here will obviously be greater than one. As a result, RB dash by RB minus one is going to be greater than zero. So, let us say that RB, the growth rate of the parent, was one, and RB dash, the growth rate of this new mutant which has come up, is 1.05.

So it's growing 5 percent faster compared to the parent, in which case the selection coefficient associated with this mutation is going to be 1.05 divided by 1 minus 1, which is simply equal to 0.05. So the selection coefficient associated with the first mutation is 0.05. Let us say, the growth rate of this is 1, as we already discussed. Let us say, for the second mutation, the growth rate is 1.03. That means the selection coefficient associated with the second mutation is simply equal to 1.03 divided by 1 minus 1.

This one is the fitness of the parent. This 1.03 is the fitness of the mutant. This one is the constant one that we are subtracting. So this comes out to be 0.03. Hence, what we see here is that although both are beneficial mutations, the benefit they confer is not exactly the same.

Some mutations confer a greater benefit compared to others, and so on. So not all beneficial mutations are equal to each other. And this is obviously going to have huge implications in terms of which mutations can replace existing ones and what the evolutionary fates of mutations will be as they occur in a population. And we'll continue building on this in the next video. Thank you.