Evolutionary Dynamics

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Lecture 33

Thank you. Hi, welcome back everybody. So, let's continue our discussion of Moran processes and calculating these transition probabilities of the system from any given state I. So, I will just quickly draw a sketch of a chemostat in a state where the number of B individuals is I. These are the number of A individuals. Their number is N minus I, and the fitness of each one of these individuals is R A. As against this, in this chemostat, there are also these B-type individuals whose number at this state is I, and the fitness of each one of these is R B.

And we are calculating these transition probabilities and trying to understand where this system can switch. So, in the last video, we calculated two transition probabilities. The first one was the probability that the system will go from i to i minus 1, which happens when a B individual dies and an A individual is born. So, this was obtained by multiplying the probabilities that a B individual will die and an A individual will be born. Next, we calculated the transition probability that the system will go from i to i plus 1, which was calculated as the product of the probabilities that an A individual will die and a B individual will be born.

But this is only half the story. There are two more probabilities, which are two more transitions that are possible in this process. And the first one of them is the probability that an individual is born and an individual dies. And in this one, what happens is that because an individual is born, the number of individuals goes up by one. But then an individual dies.

So number of individuals goes down by one. So the system which started from state i remains at state i. So this is a transition probability of the system remaining starting from state i. A birth and a death event happened and the system remains at state i. So, this probability is simply probability of A being born which remember is in the numerator fitness of all A type individuals divided by total fitness of the entire population. So, this is simply r_A times N minus i divided by the total fitness of the entire population, which is RA times N minus i plus RB times i. This gives the entire, this gives the probability that an individual is going to be born next.

$$P(A\ birth, B\ death) = \frac{i}{n}\frac{(n-i)rA}{(n-i)rA + i\ rB}$$

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$$P(B\ birth, A\ death) = \frac{n-i}{n}\frac{(i)rB}{(n-i)rA + i\ rB}$$

$$P(B\ birth, B\ death) = \frac{i}{n}\frac{(i)rB}{(n-i)rA + i\ rB}$$

This will be multiplied by the probability that an individual dies, which is simply proportional to the number of A type individuals in the population, which is N minus i divided by N. So, this is probability of transition from i to i when A is being born and an A individual dies. However, there is one more possibility where in which the system can start from state I and remain at state i, which is going to be the case when instead of A born and A dying, what is happening is that a B type individual is born and a B type individual is dying. So in that case, we have another transition probability of i to i, which is going to be B is born and B dies. So this is i to i when A is born and A dies.

And in this case, we compute probability that B individual is born and B individual dies. we write this again probability that a B individual dies. And this is going to be again by now we have done this enough times that this is simply going to be RB times I fitness of all B type individuals divided by RB times I plus RA times N minus i. times probability that a B individual dies, which is simply going to be equal to i times N. So, these are our four probabilities that we have for the transitions. Now, what you should convince yourself here is that

this i to i minus 1, i to i plus 1 and i to i because of A being born and dying and i to i, B being born and B dying, these four are the only four options if we have only two genotypes in the population. So, these four are the only transitions possible in this population when we have only two genotypes in the population, only two genotypes in the chemostat which is A and B. If that is the case, if these four transitions represent the sum total of all transitions that are possible, then their probabilities should add up to one. Because one of these transitions has to happen and these four transitions are mutually exclusive.

And by mutually exclusive, we mean that if this is the transition that is happening, that automatically means that the other three cannot happen. So the sum of these probabilities has to add up to one. So let us just confirm that the transition probabilities when sum up when these four transition probabilities when summed up sum up to 1. So sum of the transition probabilities. The sum that we are interested in is pi to i minus 1 plus pi to i plus 1 plus pi to i when it's a born and a death plus pi to i which is b born and b death.

These are the only four transitions possible. And our expressions are and these are all mutually exclusive. Mutually exclusive in probability means that if event A is happening, then B cannot happen. In the context of these transition probabilities, if one transition is happening, then the other cannot happen. So let us just try and sum these up.

i to I minus 1 is B dying and A born. So, that is equal to B dying and A born, which is N minus I times RA divided by N minus i times RA plus i times RB. That is the first one. That is this expression plus i to I plus 1, which is B born and A dying, which is N minus i upon N times i times RB divided by N minus i times RA plus i times RB.

That is the second expression. Next is A bond and A dying which is N minus i upon N times N minus i times RA divided by N minus i times RA plus i times RB. which is this third expression. And lastly, we have B bond and B dying, which can be summed up as B dying means i by N and B born is just i times RB divided by N minus i times RA plus i times RB. So these four summed up together should sum up to one if they represent an exclusive group and also that one of these four has to occur as we move forward in time.

So how do we look at this? So, if we see this, then what we are going to do is identify these terms as term 1, term 2, term 3 and term 4. We are going to add together term 1 and term 3. Note that denominator of every one of these four terms is the same. So, we can write the denominator as it is.

We get n times 1. n minus i times Ra plus i times Rb And now I'm going to add term 1 and 3. So if you look at the first and the third term, this is just N minus i into RA. Here also it's N minus i times RA. So I'm going to write, I'm going to, from these two I'm going to take this common and I get N minus i times RA. And what is left is simply i plus N minus i. i from here and N minus i from here.

So, these i's cancel and I simply get N into N minus i times RA which I am going to write like this. Similarly, I will add the second and the fourth term which has the same denominator N times N minus i times RA plus i times RB And now I should see that iRB is the common term between them. So, I am going to take that out common. And what is left is N minus i plus i, N minus i from here, i from here and these two cancel out.

So, what is left is N times i times RB. So, I can simply write this as N times i times RB. And now between these two terms, I again note that the denominator of these two terms is the same. And in the numerator, I can take N common. So what I am left with is the denominator remains the same.

Both of them have the same denominator is N minus i times RA plus i times RB. and the numerator is N and what is left inside is N minus i times RA plus i times RB what is left from the first term after i take N out is N minus i times RA which is this and when i take N common from the second term what is left is i times RB which is this So this is the final sum of all these four transition probabilities that I have. And what you should see here that this n cancels and these two cancel and I simply get one. This shows that these four transition probabilities that we have just computed here.

Is a comprehensive sum of all possibilities. That could happen in this. In this chemostat. That the system could have. Transitioned from state i to i minus 1.

Or gone to state i plus 1 from i. Or could have remained at state i. Via two different ways. One was A born, A dying. And the second was B born, B dying. So what we are going to. Think of.

We will draw a parallel between the chemostat that we've been looking at and a number line system. Which I'll just explain. We want to draw a parallel between these two scenarios. This is the chemostat that I have. And.

This is the state of the system. These are the individuals which have an RA growth rate, and their number is N minus i. Coexisting with them are the B-type individuals, whose growth rate is RB, and there are i of them. And remember, the state of the system—the variable that I'm choosing to represent everything by—is this. This system represents the current state of the system. How many B-type individuals are there?

If i is equal to one, that means there is only one B-type individual. That probably means a mutation has just happened. If i is equal to zero, that means there is no B-type individual in the population. Probably, it's been lost because of the exit stream. And if i is equal to N, that means B-type individuals have reached fixation.

They have completely replaced the black individuals that were there in the population. So, what I want us to do is think of this system in the following number line system. Imagine this number line, which has numbers going from 0, 1, 2, all the way to, let us say, i at some place, i plus 1, i minus 1. Let me write this again. I minus 1 and going all the way to N minus 1 to N. If I have a number line like this, then what you should immediately realize is that the state of the system, the chemostat, could be in any position.

That position can be represented by a point on this number line. So, if there is only one B-type individual, let us say there is a scenario when i is equal to 1. So, in the chemostat system, the state of the system is the following: there are a whole bunch of A-type individuals and there is only one B-type individual. This is the state which corresponds to i equal to 1. In the number line system, that same state is represented by this particular point.

I will say that my system is at this particular state as of this moment. Hence, The chemostat can be in any position. It may have any number of B-type individuals. Its state can be represented by one of these N plus 1 points on this number line.

You should realize that these are n plus 1 because 0 is there, and then there are N numbers going from 1 to N. The state I equal to zero represents that there are no B-type individuals. So, this state means that B has gone extinct. I equal to N represents the state where there are N B-type individuals in the population. This means B has reached fixation.

In other words, A has been completely removed from the chemostat. I equal to one is a special case where the mutation has just happened. So, the first time the mutation happened, there was only one blue-type individual, and that represents the state where I is equal to one. So, this represents a state where a mutation leading to a B individual has just occurred, removing the A so that it does not cause any confusion.

And remember, we started this entire discussion by stating that we are interested in studying the transition of the system from the state I equal to one—what is the probability that this system transitions from this state, where the B mutation has just happened, to the state where it's all B in the population. That is the transition we are interested in observing. But the Moran process has told us that this transition will not happen in just one step. You can't go from I equal to 1 to I equal to N in just one step. It's going to happen in a series of steps.

And those series of steps are given by these transition probabilities. What the Moran process is telling us is that if at any given point in time we are at state I, then from this state, one step of the Moran process can lead to four possible outcomes. The system can either transition from i to i minus 1. This happens with probability P i to i minus 1. And the numbers for this probability are something we calculated on the previous slide.

We have those numbers already. So if I know i and if I know the relative growth rates, then I know this transition probability exactly. Alternatively, the system can also transition to i plus 1, which is given by this transition probability P of i to i plus 1. And the remaining two cases give me the transition probability that the system will actually remain at i, which is the transition probability of P starting from i but also remaining at I. This, in turn, is the sum total of two transition probabilities: P i to I when A was born, and A died, and the probability of i to I when B was born and B died.

So if I add these two transition probabilities, I get the sum total transition probability that the system will remain at P i to i. And some of these Some of these four transition probabilities—the two of them are added together and represented as one here. The sum of these four equals one. That means the system has to choose from one of these four transitions. There is no other way out.

So if I'm starting from one, if the system is starting from one, which it is because when when B makes an appearance for the first time, it is at I equal to one. Then three possible steps are possible. Three possible steps may happen. Either B remains there, in which case we didn't move anywhere, or B could increase in number, which means it's taken one step closer to reaching fixation, which is our ultimate goal of fixation. We are interested in what is the probability with which a system starts from here and ends here.

So in one step of Moran process, it could either remain there. It could transition to the value i equal to 2, which means it's just taken one step towards fixation or it could take this backward step. Now, if it takes this backward step, then the game is over because then there was only one B-type individual in the population and that one B-type individual has been washed away before it could even divide. So, you are back to... you are back to a position where I is equal to zero.

And once the B type individual is lost, it's lost forever because under this framework, we are not permitting any new mutations. We are just studying what is the fate of a mutation that has already occurred in the population. And once, let's imagine that if it remains at one, then nothing really changes. we will keep on playing the same game. We started with one, we are still at one, so nothing really changes, we play again.

If it goes to zero, then the game is over because type B is lost. However, if it goes to two, then it's one step closer to reaching fixation. Early on, B could be lost from the population in just one step. One step in this direction and B would be lost from the population. But now, since the system is at 2, one step backward is not going to lead to the elimination of B.

So the elimination of B—the chances that B will get completely washed away—becomes slightly harder if the system is at i equal to 2 compared to when it was at i equal to 1. From 2 again, there are four possibilities. Two of them mean the system will remain at 2. One of them means it can go to 3, and one means it can return to 1. And so on and so forth.

So there is going to be this tug of war, and the system will oscillate between numbers. And then it will end up at either zero or n. Anywhere in between, it will keep fluctuating, and its fate will be decided by a combination of—as we will see—selection and noise. So. Let's, let's. Once again, understand this number line concept.

i, i plus one, i minus one, and minus one. Our goal is starting from here. This is our start position. and this is the position where a mutation ends when it reaches fixation so our goal is studying probability of start to end however this cannot take a big jump and straight away go to end it's going to take jumps which are of only size one or size zero remain there or go to its neighbors And through this random walk that it's going to take, we are going to, for any mutation, there are only two fates possible.

One, it's going to reach fixation, reaches fixation. Or the second fate for a mutation is that it is, it goes fixed. There is no other fate of this mutation. There are all these n minus 1 states which are available to the mutation and the system will transition through these n minus 1 states. But those are all just transient.

Its fate is not just decided. It is just being its frequency is fluctuating as it's being driven by chance events. Its fate will be sealed when it reaches either one of these two ends of this number line. And we are interested in studying the probability that what is the chance that it's going to end up at this fate compared to the other one. And that's what we are going to develop in the next video.

Thank you.