Evolutionary Dynamics

Supreet Saini

Chemical Engineering

Indian Institute of Technology Bombay

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Lecture 57

Hi, everyone. Let's continue our discussion of the Travis Hanno and Lenski paper. And in this discussion, we'll try to explore how history can impact evolution. How can we quantify the relative contribution of history in dictating evolutionary change?

So remember that what we've been discussing so far has been in the context of the following: we had an ancestral trait. An ancestral value, then we evolve the population in some environmental context, and we have the evolved trait value. And then we have this X equals Y line. Now, if this was the ancestral value, and if the evolved trait exhibited values above this line, but all at the same time, this was the case where there was selection only. On the other hand, I could have a case where the evolved lines exhibit different values but moved from the mean.

So the ancestral trait value was S naught. And in the evolved lines, the values are not the same, but all of them are above S naught. In this case, evolution is being driven by selection plus drift. On the other hand, if the evolved lines show trait values such as this, which are distributed around S0—some of the evolved lines exhibit trait values above S0, but there are other evolved lines which exhibit trait values below S0—then we say that evolution is being driven by drift only, as there is no selection because the mean is still at S0. And change is being driven by drift only.

And we can quantify these numbers by looking at the exact distribution and performing statistics on it. Now, how do we study the effect of history? We make a slight modification. Now, the ancestor we start with won't be one ancestor, but there'll be several ancestors. Let us imagine that we had an E. coli, and this E. coli evolved parallelly in different lines.

Let us say four different lines. After a period of evolution in identical conditions in these four environments, each one will exhibit a different value of the trait I am looking at. So, if I am looking at cell size, then each of these four evolved lines will exhibit a different

trait. These four different lines become the four ancestral trait values I am looking at. So, maybe line 4 cells grew up to be really large, while this was smaller, smaller, and smaller.

So, these four become the ancestral values I am looking at. When I evolve—now, there are two rounds of evolution. The first round of evolution is evolution is to generate the different ancestral trait values. So, we do this experiment, and there is bound to be spread.

So, this is like this manifesting that when I evolve, if this is the manifestation of the evolved lines, then these lines become my ancestor where each one of these has a different trait value, which is what is shown in this figure that I evolve and I get four different values and these become my four ancestors. In the second round of evolution, I evolve this as the ancestor, but I don't evolve once. I evolve this 12 times. So each of these 12 start from this particular value. Each of these 12 lines start with this value and this value and this value.

That's the starting point. And each has 12 different lines. And then after a period of evolution for T1 number of generations, I measured the value associated with the evolved. I measured the trait values associated with the evolved lines. Now, like in the previous case, I could have different scenarios play out.

Suppose, The 12 lines, so this is ancestor trait value 1, ancestor 2, ancestor 3 and ancestor 4. These can be marked here. This is X equal to Y line. So this is A1, this is A2, A3 and last

This is A4. So what could be the manifestations in this particular case? What could happen is that the 12 lines which were evolved. So just so that we are clear. So we evolve this and we get this individual.

Let's call it ancestor 1. So I take ancestor 1 and I start 12 independent flasks. 12 independent flasks. evolve it in some environment, identical treatment, let us say low glucose, for T1 number of generations. And at the end of this T1 number of generations, I measure the trait value in all 12 lines.

So this is the ancestor. So the ancestor value for all 12 lines was this A1 value, which was ancestor 1's trait value. And maybe the ancestor 1 shows values such as this. The evolved 12 lines show values such as this. Maybe this is the value that 12 lines exhibit.

When I do the same experiment now with ancestor 2 as the starting point, I evolve this for T1 number of generations. Maybe what I will see is the following. And with ancestor 3, I will see the following. And with 4, something similar. So now, what is this telling us if the response is like this?

In each one of these, there is spread. So it's not like the 12 lines are responding identically. There is not an identical response because each of these 12 lines shows a different value in the evolved lines. That means this trait is being driven by—there is a role for drift, for sure. Because if drift wasn't there, then all 12 lines, which were evolved with the same ancestor, would show the same trait value in the evolved stage.

So, there is drift. This is also driven by selection because all 12 lines have increased from their ancestor value. A4 was the ancestor value for all of these 12 lines. All 12 of them are higher than A4 now.

They are all higher by different amounts, but the point is that they are all higher. So, since all 12 lines are higher than their ancestor, this change is driven by selection also. Which is the same idea here: this change is also driven by a sum of drift and selection. Same idea here and same idea here.

So, individually looking at these four groups, evolutionary change is being driven by selection and drift within each group. How do we comment on history? History is important because when I start with A1, I can only go up to this range. When I start with A2, my range changes. A3 range changes, and A4 my range changes.

So the range is a function of the starting point where I begin with the ancestor. That is why This evolutionary response, when I compare the four groups—not individually, but collectively—I see that the average (let me plot this average here) is going up as a function of the ancestral trait value. So whatever the starting point was also dictates what the endpoint will be in this experiment. And hence, when I collectively look at this, I say that the evolutionary response in this case is also a function of history.

So, in the cartoon that is shown, change is being driven by drift, selection, as well as history. What would it look like if one of these forces was not acting? These are A1, A2, the four ancestor values: A1, A2, A3, A4. This is the x equals y line. What if the response was like this?

The first group had evolved trait values like this. The second group had evolved trait values like this. The third group had these values. And lastly, the fourth group.

So, in this case, what we are noticing is that when I look at this group, because they are different from each other, that means this is being driven by drift. Because the ancestral value was this one, A1, and the evolved value is actually much higher than A1 and is spread over this range. All 12 lines have moved in a particular direction, which means this change is also driven by selection. But in this particular case, history has no role because, irrespective of where you are starting from, the final response of the population is in the same range. Hence, history has no role. So, depending on—the point being, then—depending on when we do this experiment and depending on how we see the arrangement of points in these different scenarios, we can not just qualitatively comment on what evolutionary factor is driving change.

We can also quantify these changes as to what is driving this change. Let us do one more, and then we will close this discussion of LTEE. What is happening in this scenario? So, A1, my four ancestor trait values, A4. Now, in this case, the first ancestral value shows a response like this.

The second one, the third one, and the fourth one. So, what do we see here? We see here that in the first group, for instance, the evolved value is centered at A1.

Some lines have higher than A1 values in the evolved state, and some of these lines evolved to have lower than A1 values. The mean, however, remained the same. Hence, in this case, change was driven by drift, but not by selection. The same idea prevails in the other groups also. Let us look at one more.

If we look at the second group, the mean value of this group was A2. Some lines evolved to have the trait value elevated from A2. to something higher than A2 and other lines had this value of the evolved trait reduced from A2 to something lesser than that. But the mean remained at more or less A2. Again, the same conclusion that this is possible when drift is acting but selection is not acting and so on and so forth.

So, this is a scenario when drift and selection are not working together, but the trait value is only being driven by drift. What about history? We see that history is definitely acting because if we look at these four means, then this population has mean A1, which was the ancestral trait. This population has mean A2, which was its ancestral trait. And then A3, the third group's ancestral trait and A4, the final group's A4.

So, the responses are centered around the ancestral values that these populations starting from. And since the ancestral values were themselves different, the evolved values are

also different. As a result, this response is also dependent on evolutionary history of the populations that are participating. So, this would be a response case where there is drift, no selection, but history is relevant. So, the idea that I am trying to communicate is that suppose we were to do an experiment like this and these are simple experiments.

But through these simple experiments, we can answer questions as profound as the relative contributions of history, selection, and drift in dictating evolutionary change. And so on and so forth. So, this sort of concludes our discussion of LTE. We will now discuss a few evolution experiments that I find interesting.

I think these are experiments which, though simple, have led to evolutionary outcomes that I find counterintuitive, interesting, valuable, and intellectually very curious. The first such example is from a paper around 2010, titled The Evolution of Multicellularity. So, at the beginning of the course, when we looked at the evolution of life on Earth—this is today, this is four and a half billion years ago—we saw that life evolved fairly early. These were prokaryotes, single-celled organisms. And they continued to exist throughout evolutionary history and persist today.

Somewhere along the line, eukaryotes emerged—individual cells with a nucleus. And they have existed on Earth for about half that time. However, both of these were single-celled. But somewhere along the line, eukaryotes learned to live collectively. So, this transition from unicellular to multicellular

Happened at some point. We now know that this transition actually happened several times in the history of life on Earth. And there are several reasons why we think this transition happened, where single-celled eukaryotic cells learned to live together to form multicellular organisms. And these multicellular organisms then diversified into all the complex life forms that we see around us. If you see, we are a collection of a few 10 trillion cells—every complex organism that you see around us.

It's an organization of cells where cells have learned to coexist as an individual rather than living singly. And if you think about it, that's a great transition to have happened. So this lab evolution experiment The question is: can we study this particular transition from unicellular to multicellular

in the lab? And to me, when you ask a question like that, we need to have an experiment in mind where we can test this idea: would this transition happen? Another important

point to consider is that when we do evolution in the lab and ask a question like this, we shouldn't ask, It's an interesting question.

If it's not a task that a cell can do in one day, suppose I put the cells there and ask, will they grow, will they divide four times, and that will happen in no time. So that's not an interesting question to ask. If I ask, 'Oh, if I add one bacterium to LB media, will it divide five generations?' Of course it will. So it's not an interesting question.

But it also shouldn't be a question that will never happen. So if I ask a question, 'If I grow prokaryotes in a lab, will they evolve into eukaryotes?' Now, that's an extremely important question, but it probably won't play out in a lab setting because this event took billions of years. And we know something about why that happened, but it's probably not going to play out in a lab setting. So the question has to be just right—not too trivial, but also not so complex that it wouldn't play out in a lab in a reasonable timeframe.

So how do we do this? So we need a eukaryote to start with because prokaryotes don't form these multicellular complex organisms such as us. So we need a eukaryote. And what the authors took here is Saccharomyces cerevisiae, which is a yeast. A model organism about which we know a lot, and several hundreds of thousands of labs around the world use this. As a result, the collective knowledge we have about the workings of this organism is far more than we know about any other eukaryotic cell on the planet.

So, what is the experiment? So, remember that when we do an evolution experiment, we are actually applying a selection pressure. If we go back to LTEE and understand the selection pressure that was applied there, we allow for growth. So, growth is allowed, and then a 1:100 is transferred to the next flask. And so on and so forth.

So, the idea being—and this process is repeated over and over again. The idea being that what I'm asking the population to do implicitly when I set up an experiment like this is to say the following. That if you are an ancestor, you're like this. But if you are a variant that grows fast, then, obviously, you will divide faster.

As a result of that, your chances of making it to the next flask increase. If you divide slower, your chances of making it to the next flask decrease. And as a result, when I set up an experiment like this, who makes it to the last flask? The fast growers. If you have variations introduced in members of the population which make them grow very slow, those variations are going to be weeded out because only a 1:100 go.

99 out of 100 actually just go extinct from the experiment. So the selection pressure that I am applying here is for fast growth. And that allows me to make these observations that as time moves forward, what is the evolutionary change that I am observing in an experiment such as LTEE, where fitness, as it is quantified in terms of growth rate, increases via a trajectory like this. Early on in the course, when we were discussing experimental fitness landscapes, we saw that the first five mutations occurred.

So let us say it took this much time for five mutations to take place. The first five mutations that happened in this experiment led to a 35% increase in fitness. That is because, by the logic of this experiment, I am selecting for fast growers. To select for multicellularity, we have to change the selection pressure such that only if the cells are multicellular will they make it to the next flask. If you exist singly as a cell, you won't make it to the next flask.

So the selection has to be on a property which is accomplished better, which is exhibited better by multicellular cells rather than unicellular cells. And the experiment that I'll describe now is just a really simple experiment that these authors set up. We take a tube. And we grow Cerviciae in it.

So eukaryotic Saccharomyces cerevisiae is a unicellular eukaryotic organism. It's represented like this. It's also called budding yeast. So these are Saccharomyces cerevisiae cells present in the population. I allow growth to happen.

So this is no different from the LTEE experiment that we just looked at. So during this phase of growth, Any cell which replicates faster is at an advantage because it has a greater chance of being transferred from one tube to another. So the selection here is for fast growth. Now we saw that fast-growing cells are larger.

Larger cells tend to settle down faster compared to lighter cells. So what this team did was, instead of transferring straight away 1 to 100, they introduced an additional step in the process, which was just letting it sit. Let the tube sit on a bench for 45 minutes. So this culture in this tube was growing overnight while the tube was shaking. Shaking doesn't let cells settle down.

It also provides aeration, which aids growth. But now, before you do the 1:100 to the next tube, you let the tube just sit still on the bench. What is going to happen then is that cells which are heavier are going to settle down. And cells which are lighter will keep floating.

At the end of this 45-minute period, we sample from the bottom of the tube and transfer a 1:100 ratio of cells to the next tube.

And what is being done here is that in the first phase, when it was only growth taking place, we were selecting for fast growers, but now we are selecting for fast settlers. And the way this experiment panned out, one great way of settling fast is by becoming multicellular. Because you are larger, you settle faster, and as a result, you have a great chance of being transferred to the next tube. If you are growing really fast, but you never settle, then there is a very small chance that you will be transferred to the next tube.

But even if you grow at a reasonable speed, but you sink very fast, then you have a great chance in this experiment to become a fast settler and hence be transitioned to the next tube. We'll discuss some more details about this particular experiment and what has happened since this report came out about 15 years ago in the next video. .