Ep 108: The dialectical biologists: challenges of studying evolution in nature (with Erik Svensson)

Cameron Ghalambor 0:07

Perhaps no scientific theory has generated more controversy and has been more scrutinized than Darwin's theory of evolution by natural selection.

Marty Martin 0:15

And we don't mean by religious groups threatened by the idea that living organisms all descend from a shared common ancestor.

Cameron Ghalambor 0:21

Since the publication in the Origin of Species in 1859. Scientists from the various subfields of biology

Marty Martin 0:28

And even outside of biology

Cameron Ghalambor 0:30

Have challenged the importance of natural selection acting on heritable variation.

Marty Martin 0:34

A major breakthrough in the 1940s put a lot of these criticisms to bed. This modern synthesis showed how the principles of Mendelian genetics and Darwin's ideas about natural selection were not only compatible, they can be studied in rigorous mathematical ways.

Cameron Ghalambor 0:47

But there remains skeptics.

Marty Martin 0:49

And to this day, one of the lingering critiques is the divide between small micro evolutionary change within populations.

Cameron Ghalambor 0:56

Imagine individual variation in the size and shapes of finch beaks

Marty Martin 1:00

And larger macro evolutionary changes observed between species

Cameron Ghalambor 1:04

Imagine the difference in the beak of a Finch versus a flamingo.

Marty Martin 1:08

Another critique is that not all evolutionary genetic changes due to natural selection, people like Motoo Kimura showed that a lot of variation at the DNA sequence level is effectively hidden from natural selection. Maybe this variation could lead to those sleeping beauties that we discussed with Andreas Wagner late last season.

Cameron Ghalambor 1:24

Perhaps one of the most famous critiques happened in 1979 when Stephen Jay Gould and Richard Lewontin published the Spandrels of San Marco paper, where they accuse the field of evolutionary biology of simply assuming without evidence that most traits are adaptive.

Marty Martin 1:39

They compare an evolutionary biologist to being no different than Voltaire's fictional character Dr. Pangloss, who believed our noses evolved to a hold up our glasses. They argued that like the non-functional architectural spandrels at the top of an arch and ceiling, many traits that seem adaptive might not be.

Cameron Ghalambor 1:55

Only a few years later, in 1983, Russ Lande and Steve Arnold published the landmark paper that provided a statistical method for measuring selection on correlated traits. This paper fundamentally altered how evolutionary biologists approach the study of evolution in natural populations and added that missing rigor that Gould and Lewington sought.

Marty Martin 2:16

Our guest today, Erik Swenson from Lund University in Sweden recently published a perspective paper revisiting this landmark publication.

Cameron Ghalambor 2:23

We talk with Erik about the legacy of the Lande Arnold paper, and some of the challenges of applying it to studies of evolution in natural populations.

Marty Martin 2:30

We also talked about how many of the critiques of evolutionary biology can be understood by the feedbacks that occur when there is reciprocal causation between interacting populations, or between populations and their environments.

Cameron Ghalambor 2:42

And about the philosophical underpinnings of evolutionary biology, and how this plays out in some of the critiques leveled against it.

Marty Martin 2:49

I'm Marty Martin.

Cameron Ghalambor 2:50

And I'm Cameron Ghalambor

Marty Martin 2:51

And this is Big Biology.

Cameron Ghalambor 3:03

Erik Svensson, thanks so much for joining us today on Big Biology. We're really looking forward to talking to you about your research, your perspectives on the challenges of studying evolution in natural populations, your thoughts on the current status of evolutionary theory, and where do you think the field is going. And I think to start off this episode, for full disclosure, I should start off by saying I've publicly referred to you as my favorite evolutionary ecologist, because we share a lot of research interests. And we both started our careers working on birds, and then we've moved into other organisms. And so I'm really looking forward to getting your perspective and to see how similar and how different it is from my own.

Erik Svensson 3:45

Thanks. I'm happy to be here.

Marty Martin 3:47

Excellent. And the same thing, Erik, I mean, it's been great to have you engage with us through social media as a podcast. Like Cam, I've been a big fan of your work for a long time. So to see you be supportive of the show, and then, you know, constructively critical when when you're not a fan. That's what this is about. That's how science is supposed to work. So thanks for that.

Erik Svensson 4:08

Yeah, I would even say so in my case, Big Biology is probably one of the few podcast I follow. So I have to compliment you for that. Great.

Marty Martin 4:17

Great thanks.

Cameron Ghalambor 4:18

All right. So let's jump into one of the kinds of big topics that we have on hand today, which is evolutionary theory. You know, modern modern evolutionary theory is, is built on this very strong foundation, theoretical foundation in population genetics, quantitative genetics, and describes the processes that shape, you know, genetic variation over time and space. But for those of us who work in natural populations, there are all these very complex interactions with the environment and a lot of these interactions can really complicate the study of evolutionary change. But you recently wrote this prospective paper on the impact of the Lande Arnold 1983 paper on measuring selection on correlated characters, this very landmark paper. And this paper, as you point out really provided a tool for people who work in natural populations to embrace sort of some of the, you know, basic core evolutionary theory ideas and put it into practice. So, can you give us a little just introduction on the importance of this paper and the state of the field before 1983, and then how it's changed in the years since this publication?

Erik Svensson 5:43

I'll try not to reiterate my whole paper, but I'll try to summarize this paper is a very important paper, it's very well cited thousandss of citations. I published it this year in Evolution, and deliberately this year because it's 40 years since it came out. And there has been a tradition in the journal Evolution to have this "What have we learned in 40 years?" papers. Because our field is very slow moving, I would say it's a very conceptual field, it takes a long time.

Marty Martin 6:18

Very gradualist, would you say?

Erik Svensson 6:19

Yeah gradualist, or even stasis some time, perhaps. It takes a long time to see the impact. And this paper- well, first of all, it's very important to see the timing it came out in 1983. And re-reading it again, especially the introduction, you can see that it's partly stimulated, like Russell Lande and Steve Arnold, who wrote this paper, they were partly stimulated or provoked, if you want to say, by another famous highly cited paper Gould and Lewontin 1979. So those two papers, they have kind of one stimulated the other explicitly so they say in the introduction. And for those younger listeners, most evolutionary biologists should know the Gould and Lewontin the famous the spandrels paper, the spandrels on San Marco and the critique of the adaptation program or the Panglossian paradigm

Marty Martin 7:18

The Panglossian paradigm. Yeah, we talked about this in my evolutionary medicine class just yesterday, as a matter of fact.

Erik Svensson 7:23

Yes, yes. And we read that paper last autumn in my lab group, and then we read Lande Arnold, which came four years later, because I wanted the students to get the feel for, for what the debate was about. And that discussion about the Lande Arnold actually helped me to write this perspective article. So in short, Gould and Lewinton criticized what they saw as excessive adaptation is speculative adaptation is poor science, that you assume adaptation and selection, but without showing it. And Lande Arnold felt that they, by providing a recipe how to estimate selection using fitness data using data on traits, and using regression methods, which are very basic, not very sophisticated today, with all our statistical methods, they felt that they provided a constructive way of avoiding to go into this adaptationist trap. I even had a quote of them, where they cite Gould and Lewontin and say that this is the best measuring selection directly, and quantifying it's the best way of increasing rigor in evolutionary biology. And then this became very popular, the use of regression methods, going out and looking for fitness differences in the natural population measuring traits became almost what some call what we call a cottage industry. Especially in North AmErika, it became very popular to go and do these selection studies. But it was also criticized by some. It was more popular in North AmErika than in Europe, especially in Britain, where another research tradition, namely the Krebs and Davies, the Behavioral Ecology tradition was more prominent. So it seems like there was hesitance in Europe and Alan Grayson, theoretical biologist, he even had a very critical chapter in a book in 1986, by Clutton-Brock, where he criticized this Lande Arnold method, because he thought it's just correlational you should do experiments. And he even labeled them in a little bit condescending fashion, "The Chicago school of evolutionary biology," which was not not not a good thing, because the real Chicago school is that the neoliberal economics under Milton Friedman, so calling something a Chicago School, I don't think that was a compliment.

Marty Martin 10:06

It was not meant to be a good thing.

Cameron Ghalambor 10:08

Although among evolutionary biologists, I think the Chicago School definitely, we knew who was there.

Erik Svensson 10:16

Yeah, that was the important Chicago school. But anyway, this has resulted in a large body of work where people have estimated selection in natural populations. And then, in 2001, Joel Kingsolver and colleagues did the first meta-analysis where they asked the simple question: H"ow strong is phenotypic selection in natural populations?" And this was followed by several other meta-analyses, one which I was involved in. So the legacy of this paper has clearly been that we have learned a lot about selection, the strength of selection on phenotypic traits in natural populations, much more than we could before because we didn't have any metrics or quantitative methods to do so.

Marty Martin 11:17

So Erik, I want to ask, we want to get into some of the details of what they provided. How has it contributed to the development of evolutionary theory? And where is evolutionary theory going? So for us to do that, I think we need to dig into some of the details. And I'm going to say a little bit about what I understand to be the history and the papers that you've written on this, what we're discussing today, fantastic. It's amazing the diversity and the amount of things you've been producing on these things for the last several years. So that's really made it easy for me to summarize, Gould Lewontin criticize the adaptationist paradigm, maybe there's more to think about an evolution than just walking in and assuming that everything is some sort of adaptive trait. Lande and Arnold, come up with a method for quantifying studying selection. But that's an embellishment on the price equation, right, which had been around before and was a simpler version. Maybe you could say something about that, because I want to get us to what they did specifically, that has opened up these new doors that led Kingsolver and others to do the meta-analyses. So how do we get to a G matrix? How do we get to this variance, covariance exploration? And what is it about selection they were doing with regression that was different than others?

Erik Svensson 12:22

First of all, there were methods to estimate selection before, but they were mainly univariate, they were based on one trait at the time, we know that selection operates not on one trait at a time, but on multiple traits. And sometimes, not only in a linear fashion, also stabilizing and disruptive selection, and sometimes also on combinations of traits, which we call correlational selection. So the textbook way of teaching selection, tends to be you compare survivors and nonsurvivors with respect to mean, but selection can also operate not only on means, but also on variances and combinations. So I think it opened up the door to the multivariate view of selection, that selection is a multivariate process. And that the response to selection is not because only direct selection on a trait, but also indirect selection due to correlations with other traits. Yes, I think that is a very important thing.

But then you also mentioned the G matrix. And I think here is one one interesting thing with the Lande Arnold school and their approach in general is that they state very early on, and I think this is almost sometimes forgotten, that selection and inheritance are distinct phenomenon, they can start be studied in isolation. Tou can actually study selection without knowing anything about the G matrix of your organism. And I would say in most organisms we study, it's terribly difficult to get a G matrix or even a simple measure of heritability. But it's still valuable to study the process of selection to give us an idea of the strength of selection. There is also quote, in my perspective article by Ronald Fisher and his book from 1930. The first sentence says: "Natural selection is not evolution." And I tend to think that is very often forgotten. And that selection is a within-generation ecological process that can be studied without regard to genetics at all. And I think this is maybe the main importance of Lande Arnold, it suddenly opened up for ecologists who typically don't, either don't have genetic information or are not even interested, to contribute to the evolutionary literature by realizing that we separate inheritance and selection. It also brings in, it's an attempt to bring in, the insights from the plant and animal breeding literature and the experience they did there to natural populations with mixed results, I would say.

Cameron Ghalambor 15:10

So Erik, I have a question that, I want to ask you, because you mentioned correlational selection. And I know that's a topic that you've been very interested in. So just to restate, correlational selection is selection that favors particular combinations of traits together. And so that's on the selection side. And then we have the the G matrix, which captures how traits are both genetically correlated and how much genetic variation exists for that trait itself. And so, one thing that's always perplexed me, and I'm curious to get your opinion on is that, on one hand, we when we separate selection from inheritance, and we look at the G matrix, it's often assumed that these genetic correlations and the variance covariance matrices are stable. And they represent a constraint on the response to selection. But at the same time, if there's correlational selection on combinations of traits, shouldn't then the G matrix itself be the subject of selection? And aren't the patterns of variances and covariances? Also shaped by selection? It seems, it seems to me like those ideas are kind of in conflict with each other. I'm curious what you think about that?

Erik Svensson 16:35

That's an excellent point. And I think you're right, they are partly in conflict. It's an idealization, that is maybe necessary to do for operational reasons, to estimate selection. But of course, you're completely right. And I completely agree, I've even written about this, that the G matrix should not be viewed as it may be was in the past, mainly as an evolutionary constraint. But it's also partly a product of selection, genetic correlations between traits reflect past and, to some extent, probably also ongoing selection. And I think this is a very, I mean, we all three of us are organismal biologists, I hope so I don't think so we are not naiive reductionists of the caricature kind that Gould and Lewontin criticized, you know, that you're atomized the organism and see it as only the sum of its parts. The interesting thing with biology is that organisms function together as some kind of more or less integrated wholes. And these these kind of interrelationships, genetic correlations don't, or shouldn't just be viewed as kind of something negative, but also something that's promoted by selection. This is something that becomes very obvious when you work, when you do research, empirical research, as I do and have done on systems where you have two or several discrete, genetic morphs, like color morphs or something else. Because there, you actually see two or more clusters within a species, which are so to say, reasonably adapted to what they are doing. And selection favors the two or more adaptive peaks within the adaptive landscape, so to say within a population. Ir's good, you pointed out this inconsistency, Cameron, because there is a maybe your next question will be about reciprocal causation feedback. If the G matrix is evolves, partly by natural selection, and then it could feed back on selection in turn. So there could be a two-way street. So to say, and most likely is

Marty Martin 18:44

These concepts are hard to talk about without images, and a lot of a lot of build up, so this is a risky question. We do want to get to reciprocal causation, but a risky question first, how are you now thinking about epatasis? Because that's not really well captured in G matrices, as I as I understand it. But then if I can make it even more complicated, because I know it's a recent interest or longtime interest of yours in a neat new paper on the damselflies, the role of plasticity and its sort of relevance to the Lande and Arnold paper and how we now think about selection?

Erik Svensson 19:16

Yeah, so first of all, epistasis is something I think we all struggle with, even those who kind of are specialized on it. We're talking about the interactions between genes, and that by itself is very complicated. For me, I need to have a visual model to understand it. But maybe first I would, I think it's useful to distinguish between fitness epistasis and epistasis in general. Fitness epistasis is when a dependent variable is fitness, survival or reproductive success. And it's affected by two or more traits that interactively affect fitness. That is a form of epistasis with the effect of fitness is more than the sum of the two traits they actually interact. And we can visualize this as a curvature in the fitness surface between two traits. A famous example that many evolutionary biologists and ecologists know of is Butch Brodie's garter snake who differ in in both coloration and predator escape behavior and where different combinations are associated with different fitness, there are essentially two peaks. So when it comes to fitness epistasis I think, in quantitative genetics, I think that it's simply selection, operating. And it's the cross product, the interaction term between two traits. When it comes to epistasis, physiological epistasis between two gene products which affect the trait, yeah, that is.

Marty Martin 20:52

Staggeringly complex?

Erik Svensson 20:56

Yeah, that's something which quantitative geneticists struggle with. But I guess one answer to that is that physiological epistasis has both a statistical meaning, a component to estimate, but also a physiological meaning. In an isogenic, Drosophila strain, you still have epistasis, because genes interact. So I guess that's very down into the rabbit hole, like, do you want to dig deeper?

Marty Martin 21:23

Well, we're gonna I think we'll come back to things like this later. I mean, it's right now to say that this is really complicated would be fine, because when we start to talk about reciprocal causation and some other pieces, I think it'll it'll come full circle, so we don't have to go into it.

Erik Svensson 21:36

You should invite Trudy Mackay.

Marty Martin 21:38

Yeah, we've talked about that. We we had a conversation years ago with Mihaela Pavlicev on this topic, too. T he more complicated something is, the more fascinating I find it. This is almost intractable. But how about plasticity? So maybe the way into that topic, tell us about this, this recent study, this amazing study, across all of Sweden that you did with so many different species of damselflies it was in Ecology Letters.

Erik Svensson 22:06

Yeah, plasticity, both you two are interested in plasticity. The relationship between plasticity and selection I, I've been thinking about, and of course, now, it has been quite popular the, over the last 10 years, these theories of plasticity first. That plasticity can play a initiating role in adaptive evolution so that an organism can invading a new environment such as a range expanding insect, for instance, and encountering a harsh novel environment, and it can survive by plastically adjusting its phenotype. And then later on, this plastic phenotype is genetically assimilated. So the trait becomes assimilated. I mean, these are very popular ideas. And very, I would say hot topics, for those who want to see greater role of plasticity. In this particular damselfly study, we did together with a former postdoc of mine, Stephen De Lisle and Maarit Mäenpää, we were interested in thermal plasticity with respect to phonology. And we combined data from one species, where we have could do some quantitative genetics, with the data from other species and citizen science data, and find there seemed to be a role of plasticity and range expansion, taking phylogeny into account, maybe that's one example of where plasticity can play a positive role driving adaptive evolution. But I would also say, before Cameron jumps on me, I'm increasingly also thinking of non adaptive plasticity or even maladaptive plasticity. And I think maybe there has been a tendency to assume that all plasticity is adaptive. I'm not so sure anymore, I think we can say for sure, there is lots of plasticity. But how much of that is adaptive? And how much is maladaptive? I think that's a very open question.

Cameron Ghalambor 24:27

Yeah, so the question I had kind of touches on what you were talking about, on the relationship between plasticity and selection, and evolutionary responses. So my understanding of that paper was that you found that- Well, I think first you showed that over the last, I think, 18 years damselflies are emerging maybe ten days earlier than they previously were, and that the plastic response to warmer temperatures is to emerge at an earlier time. And so the plastic response, I think the words you use is very aligned with the sort of evolutionary response that you see within and, and obviously, also between species. But the question I have for you is that well, that type of plasticity would seem to be adaptive. Because it, it's sort of aligned with the evolutionary response that you would expect, if that's what selection is favoring. But what I'm confused about is if you can solve the problem of a warming environment through plasticity, shouldn't there be fairly weak selection to evolve? If you can get closer to that adaptive peak just through your plastic response to temperature? That would seem to me to weaken the selection differential, and then that should actually slow the evolutionary response.

Erik Svensson 25:55

Yeah, yeah that's something I've been thinking about a lot, too. But this is a general question not about this paper, I suppose. And I agree that it's somewhat of a maybe, a contradiction in plasticity research. On the one hand, plasticity is supposed to accelerate evolution as a pacemaker, or whatever we could call it. But exactly as you point out when it comes to temperatures, I mean, you had Martha Muñoz on this show before, right, and she has done very nice work on Anolis lizards and showing that they thermoregulate, a form of plasticity, and thereby make evolution slower. Yeah, she probably talked about the Bogert effect this fantastic paper by Ray Huey. It's also one of my favorite papers, by the way, and it's, it's almost like you have have to, you have two opposite views of plasticity. And, maybe, I wish I could solve it, but I think it's something we need to think deeper about, including myself. So I guess it's somewhat paradoxical, as you say. One aspect, though, is that it's not only about the strength of selection, but if plasticity also facilitates population size, enables a species to have maintained larger population numbers under harsh conditions through plastic adjustment, it also means that population size is not reduced as much. And thereby the strength, the efficiency of selection increases. Even if selection doesn't change, selection becomes more efficient at the larger size. So that could partly help us to partly solve this contradiction you mentioned, Cameron.

Cameron Ghalambor 27:53

One last question on this topic, I guess is that thinking about plasticity, and particularly in the context of the Lande Arnold equation, one thing that we learned in quantitative genetics is that heritability is very context dependent. It's dependent on the environment in which you measure it. But then when we talk about genetic correlations, and the structure of the G matrix, all of a sudden, the context dependency never enters the equation. And yet, there's a lot of papers that show that even genetic correlations are plastic. And so the underlying genetic architecture seems to be sensitive to the environment that you measure it in...

Erik Svensson 28:35

Oh, what a wonderful understatement.

Cameron Ghalambor 28:42

And then I think back to the, to the, to the selection part, that you were just talking about, if plasticity in the environment induce shifts in the distribution of the phenotypes, relative to some optima, it's also influencing potentially the strength of selection. And, you know, I can say personally, I've become a little bit frustrated by like, the terms genetic assimilation and genetic accommodation. Because I think, if we could think about plasticity more in the context of Lande Arnold, and have a better understanding of how the environment is affecting those parameters that we're trying to estimate natural populations, I think we could make potentially more progress on a better understanding of how natural populations deal with environmental variation and how that influences evolutionary responses.

Erik Svensson 29:40

It makes a lot of sense. It's funny also, you mentioned, you challenged me on this damselfly study and about plasticity and selection. It just reminded me now when I checked it, we have a graph, unfortunately, this journal Ecology Letters like many other journals, they have this limited number of figures, and all the interesting stuff you have to check in the supporting material these days. It's not I mean, I would wish we could go back to like, well, everything should be published in Ecological Monographs or something, 50 pages. That's actually a journal where I've actually been rejected once because the paper was too short.

Marty Martin 30:19

Yeah, that's a rarity.

Erik Svensson 30:22

But in that paper, we actually estimated selection on phenology. For this, our target species in southern Sweden, the common blue-tailed damselfy. And in spite of that plastically change, the annual selection gradients were quite weak. So it fits well with what you're saying that plasticity masks selection or plasticity dampens selection.

Marty Martin 31:01

I want to talk about another paper, Erik, and I think it's going to help us conceptually tie what we started with, with some of the ideas that other guests of the show have talked about. In 2018, you wrote this paper on reciprocal causation. So before we get into the nitty gritty details of that, tell us what you understand that to mean, and then maybe give us some examples, the examples that you wrote about in the paper are, of course, fine.

Erik Svensson 31:29

Yeah. Oh, now we're moving into the philosophical realm. And this is something that I think many of us are thinking about, and I, and we should think more about reciprocal causation is sometimes called cyclical causation. And in the philosophical literature, it's like when an effect becomes a cause. So there's not a strict linear causation, so cause and an effect, but the effect then becomes a cause. And then it goes around and around. Many philosophers struggle with this, I guess I'd been a bit naiive, because for me, that's a natural way of thinking, I think we all, evolutionary ecologists especially, everything affects everything, and it goes back.

Marty Martin 32:16

And this is what we do, right?

Erik Svensson 32:19

Good examples of this are maybe co-evolutionary arms race, you know, a predator exerts selection on a prey, and the prey evolves to escape the predator. And that feeds back on the predator and so on. There are other examples. Frequency dependent selection is another example where you know, a genotype or phenotype has a certain fitness, and as it increases, because of selection, it increases in frequency. But since fitness is frequency dependent, the composition of the population changes, and that feeds back on the fitness of the genotype, so it gets low fitness or high fitness, if it's positive frequency. So there are many of these situations. And one very popular field that both Cameron and I have... well, I was actually quite late in publishing my first paper where I use the term eco evolutionary dynamics, it wasn't until 2019, so I was the last, last resisting, but then I wrote my first paper with ever equal evolutionary dynamic, so now I guess I am in the boat with everyone. That's another example where you have the feedback between ecological processes like competition, and evolutionary change, like, like ecology and genetics, or ecology and evolution interact. So that is what reciprocal causation means to me, in an evolutionary ecology context.

Cameron Ghalambor 33:44

So yeah, so I think, but part of your motivation for writing about reciprocal causation was in part because some of the criticisms of the standard evolutionary theory is that it sort of leaves out certain processes like niche construction and potentially plasticity in agency. And you argue that those topics, which some people have argued are left out, are actually well represented under this sort of umbrella of reciprocal causation. Can you maybe talk a little bit more and unpack what you mean by how those processes sort of fall under this larger umbrella?

Erik Svensson 34:28

Yeah, now we're also entering this debate that has been going on for maybe the last eight to ten years, or actually longer back in 2007. I think Massimo Pigliucci published this paper on do we need an extended evolutionary synthesis and it has been a debate that has been taken place, not only in the evolutionary biology community, but also on blogs, on Twitter and in popular media and so on. And I wouldn't say that it has been all bad. I think it has been interesting and challenging to think, but there is also sometimes you get the feeling it's a storm in a teacup. And I think many of my colleagues, which I respect a lot, they feel that the current evolutionary framework is incomplete. And it leaves out many things, including reciprocal causation, niche construction, non genetic inheritance, plasticity, and so on a range of interesting phenomena. And I agree very much these are very interesting phenomena. And especially maybe reciprocal causation and feedbacks is something we really need to think about.

But then, in this criticism of what's sometimes called Standard Evolutionary Theory, and the more I read about it, the more confused I get about, if there even exists something that that we can meaningfully label as Standard Evolutionary Theory, regardless of which position we take in these debates. Because what's often often coming up is the so called modern synthesis, this this framework that emerged from the 1930s to an ended in 1950s, the synthesis between Natural History, Darwinism and Mendelism, this modern synthesis is often criticized by those who want to see reform against a more modern version, where we are starting to talk more about these things that are presumably left out of evolutionary theory, and that includes reciprocal causation, they claim. I feel that description of history is not is somewhat misleading. This can easily become an identity, political debate: Are you for or against the modern synthesis? I think I'm not neither for or against. It's something that happened. It's a very important part of our history. But we have moved beyond it.

I think it's interesting to discuss what was missing from the modern synthesis and what we have, what we need to incorporate today. But I would say it's slightly misleading, as has sometimes been made, particularly by Pigliucci, in 2007, that we still live in the modern synthesis here, I would argue we left the modern synthesis already in the 70s. So we we have been living in a post-synthesis era for quite a few decades now. While I agree there, the modern synthesis was incomplete, in some sense, it left out developmental biology, for instance, that's the most famous example. I would also say there are other criticisms one could have against the modern synthesis that you typically don't hear from the reform camps, so to say. I t's striking when you read the literature about the modern synthesis, for instance, how none of the architects, Mayr, Dobzhansky, anyone even tried to estimate selection, it was just assumed. There were not many field biologists Ernst Mayr never did, to my knowledge, any field biological study where you actually went out in nature, marked things and looked at survivorship. So ecology was also left out to the modern synthesis, but it has kind of gradually entered evolutionary biology from the 60s and onwards. And I think it's a process that's still ongoing.

Marty Martin 38:38

Well, these are fair points, Erik. And I mean, you said, you've listened to a lot of the show. So it's clear that we have touched this topic many different times. I mean, it's been useful for me to do this show, because it's helped to, I think it makes me feel like my thinking is clear on these topics. I wonder what you think about the slight change in, I don't want to put words and folks' mouths, but maybe the push for an update, an extended evolutionary synthesis? To me, I think what people what I read people to be asking for, is, let's make efforts to develop a cohesive single theory of life. right. Which, you know, inherently includes evolution by natural selection, the modern synthesis variants thereof, and all the niche construction bells and whistles and such. I mean, is that a reasonable thing to ask for? Or is that so like epastasis, so grandiose that we can all agree, but we can't make progress?

Erik Svensson 39:36

That's a very interesting question, because that is what do we want our field to be? Do we want some kind of grand unifying theory? Or do we accept that our field is somewhat fractioned, consisting of several coexisting schools or research traditions that are partly, but not fully overlapping? I tend to lean, maybe this is slightly pessimistic. There is science philosopher Imre Lakatos, you probably have heard about, who tried to find a middle ground between strict Popperian is with its falsification criteria and coons paradigm theory, which has been accused for being very relativistic. And neither Kuhn nor Popper are very satisfying, philosophers, at least to me, if you want to understand how science works, I mean, we know we don't get well to try to falsify that we tried to find out new stuff, right? So no evolutionary biologist, I know is a strict Popperian. But we are neither, I think would be relativistic Kuhnian. So we think, "Oh, I changed paradigm, now I'm doing something completely different from last year," we still maintain some continuity. And Imre Lakatos he suggested that science consists of several coexisting research programs, each with a core of strong assumptions. And then there were axillary hypotheses called, like a protective belt. And that's increasingly my view of evolutionary biology, that we have these research traditions, and that's okay. Maybe that their modern synthesis view, which was at that time very important step that you could unify every biology in all its details, maybe, maybe we will have reached this kind of creative chaos. And will remain there .

Marty Martin 41:39

Well, so I'm curious, let's just juxtapose it against our sister science, physics, that does have some version of a grand unified theory. I mean there's plenty of problems we're well aware of, it's not fully resolved. Most levels in physics are cohesive, you know coherent. What is it about biology that makes it different? That it's not possible?

Erik Svensson 42:04

Yeah. Well, I think we can agree on a few. Natural selection is controversial, that it existe. I guess our question is, rather its reach, how much can we explain by natural selection? But then we probably have, there's probably disagreement with what should count as an evolutionary process and what is rather an outcome of selection? In that sense, maybe I'm a traditionalist, I tend to think of the evolutionary processes in quite strict sense. What Elliott Sober the philosopher of biology said the Consequence Laws: natural selection, or sexual selection included genetic drift, recombination mutation, these, what some call, "forces." And then I think of a lot of other interesting stuff like ecology, predation, temperature, whatever we study, I think of those more as source laws, they are behind, so to say the consequence laws, but they are not evolutionary processes in themselves. Competition and predation are kind of ecological phenomena, extremely interesting phenomenon. But their influence on evolution is that they give rise to selection. I also think we need to distinguish between source laws, consequence laws and evolutionary outcomes. And sometimes it's difficult to distinguish them. But I tend to think, although I'm not dogmatic about this, that phenotypic plasticity is partly an evolutionary outcome of selection, either strong selection that leads to cannonization or weak selection, when more plasticity might be permitted, for instance. But then, of course, we have, as Cameron alluded to, plasticity, can feed back on selection, weaken selection, so then it becomes more complicated.

Cameron Ghalambor 44:02

Well, I think it fits in nicely with, you know, the ideas of reciprocal causation, but also something that you said, I think, that resonates with me is, you know, as a traditionalist, you see sort of consequences or outcomes of selection. And I think the topic where that fits in, and is most interesting, I think, because of a lot of the debates that Marty and I have had recently, is about the concept of agency. And I kind of I think as from that traditionalist perspective, see agency as a consequence of selection, which then also has the potential to feed back. Whereas I think an alternative perspective is maybe that this type of goal-oriented behavior can somehow occur in the absence of, as being a not a consequence of selection, just sort of a property of living organisms that just sort of is there. I know you've thought a little bit about agency, is that consistent with your thinking? Or is that different?

Erik Svensson 45:04

I view agency as an outcome of selection, that selection tends to create organisms which behave in an adaptive way, whether it's homeostasis, or goal searching, or finding food or whatever. So I tend to think of, not agency as primitive or ancestral, but rather as derived character, that agency is a product of selection. I think those who argue for agency to see something more like I think, Denis Walsh, the philosopher was on this show, I think he views agency as maybe more an ancestral feature independent of selection. I struggled to see how you can have an agency without selection, I'm quite skeptical, but I'm willing to change my mind if somebody could show convincingly that this can exist. But let me just say, give a little bit of a warning here, when we talk about agency. We talked a little bit about plasticity, and whether it's adaptive or non adaptive. And I think we should not forget the message from Gould and Lewontin, about avoiding falling into the adaptationist trap. To interpret what we see in nature as being functional, being good for the organism, being adaptive. I think there is still some criticism that is valid. That was a criticism against naive Sociobiology and Behavioral Ecology, that we assumed that organisms do this and that and they are perfectly adapted to their environment. And I would say, that has been a very successful assumption in much of optimality, biology and Behavioral Ecology, and organisms are extremely well adapted. But there are also notable examples when they are not.

And my favorite example, if I can go back to my favorite insect are dragonflies and damselflies. And I just got a WhatsApp message from a former student in India, who saw a car with its windshield, and she saw a dragonfly female trying to lay eggs on the windshield. Because it thought that the windshield was water, it was lured. That's what we call an ecological trap. The dragonfly female thinks she lays eggs in water, but she dumps her egg on a hot windshield, it will be maladaptive. So the dragonfly female there in that case, has some agency but it's obviously not very functional. It's goal oriented, but it leads wrong. You could argue the same with moths flying into light. I have a light trap and catch moths.

Marty Martin 47:48

Are humans eating too many cheeseburgers, right?

Erik Svensson 47:52

Yeah, exactly. There are definitely situations where I think agential thinking that can be very successful can also lead you in the wrong direction.

Marty Martin 48:06

That's really interesting, Erik. So I'm obviously a big fan of this concept, hence, Cameron and my never ending, we'll call them conversations, they're a little more heated than that sometimes. But that's what friends do. I don't think of agency as exclusively adaptive. In fact, I mean, I was so excited to see your paper on reciprocal causation, because I thought I was going to read you to say, agency is just a form of reciprocal causality. What's the problem? Let's, get excited about this. There's an interesting part of your paper, so as Cam set up, it is written in response to the calls for the extended evolutionary synthesis. And you present the nice examples, well, reciprocal causality is a common thing for a lot of biology. We all study it. And you say that Kevin Lala and colleagues, this was specifically in response to something that that group had written. They said that the reason for an extended evolutionary synthesis was the need to address organismal agency. But then you proceeded to give examples that were, you know, eco-evolutionary dynamics, host parasite, predator prey arms races, and that's all fine. But why didn't I was just wondering why there wasn't an example or a sort of deconstruction of the idea that organismal agency was reciprocal causality? I mean, isn't it?

Erik Svensson 49:23

Very interesting that you say, I have to admit that in 2018, or other 2017. When I wrote this, first, I hadn't thought about the concept of agency a lot. I should search in the paper, but I don't think I use the word agency at all. It was just a few years later, I actually read Denis Walsh book about agency and now agencies all over. Yeah, so I have to say I haven't written explicitly about agency, maybe I should. The way you formulate, it as agency is reciprocal causation. I need to digest that a bit.

Marty Martin 49:59

Well, there's a couple of episodes where we've talked a lot about this. Dan Nicholson, Sarah Walker, Paul Davies, they talk a lot about information. And so I don't know if you listen to our episode, it's Cam's favorite, the one that we had with Karl Friston about the free energy principle. I mean, that conversation crystallized for me better than anything else. I mean, I think because it was so explicit. And it's sort of mathematical, it was mathematically explicit. It helps to put some structure to what agency would look like, and maybe even how we measure it.

Erik Svensson 50:32

I think I need to read that. I mean, we need to analyze the words and are what we're talking about. But I think I have to humbly admit that my own thinking changes the whole time, it should be unless you're very dogmatic. But I think it's interesting to think about organisms. Something interesting in this debate is that we tend to focus evolutionary biologists on either genes that's molecular evolution and molecular biology, or populations, which I guess is the traditional focus that I belong to. But the individual organism sitting in between is also interesting. And I agree with that. And I also agree that organisms are interesting, and somewhat paradoxical. You have had Arvid Ågren here on this show. I just struggle a little bit. And maybe that's because I'm a statistically oriented evolutionary ecologist, how do we develop a rigorous empirical research program on individual organisms? Because we need sample sizes we need? We need to generalize.

Marty Martin 51:42

Yeah. And that's a fair question, that is a great question. And that is one of the most difficult that's the biggest. one of the biggest challenges as I see today. But yeah, great point.

Erik Svensson 51:51

Yeah and I think also, I would say, also that paper on reciprocal causation, it was not only in response to Kevin Lala and colleagues, it was also partly an obituary to Richard Levins, who passed away. And Levins and Lewontin. Were quite early on with these ideas in the book. I don't know if you have read it. The Dialectical Biologist from 1985.

Marty Martin 52:19

I hadn't read it. I know of it. Yeah. But I've never read it.

Cameron Ghalambor 52:21

I have a copy. Yeah.

Erik Svensson 52:24

Yeah. And that is an interesting book. It was my postdoctoral advisor who told me to read it. It's a very interesting book. Apparently, the evolutionary biology community is still very divided about Lewontin and Levins, because they, because of this heated debate about sociobiology and, and Marxism and the Cold War, that all went on in the 80s.

Yeah, yeah, it is interesting, because I guess I wanted to bring this question up, too, especially in the 1970s. It seemed that the seperation between science and politics, and maybe further in history was much smaller. And that I think scientists today tend to be less open or try to be less open about their political leanings, because it might, for example, imply that, you know, you have a bias in one way or the other. But one thing that you're very quite open about your political leanings and, and certainly the Dialectical Biologist, Levins and Lewinton were very, very open about that type of thinking and that type of approach. And, and so I guess I'm curious, from a sort of a philosophical way, how you see that type of dialectical thinking, influencing the way that you do your own science and how you ask questions and how you approach the questions that you ask?

That is very interesting question. And I think many biologists should think a little bit more about their worldview and why they do things and thinking about it. Again, I think Marxism of course, can mean a lot of things. It can be this

Stalinist dictatorships in the Soviet Union with very politicized institutions, Lysenko, and all those horrors. But it can also mean and I think in in parts of the Dialectical Biologists not all of it, you can actually see a very refreshing analytical way of viewing the world and thinking about these cause and effect and feedbacks and zooming out and seeing things from different perspectives. So I think that book has sometimes been ridiculed and unfairly criticized because they are, at least in some chapters, they are fairly balanced. And they also admit that liberal or bourgeois science, as they call it, have also made important contributions. Game theory is one of those examples they mention explicitly. So I think being open about your own views and not trying to hide them is, in a way, more honest than just pretending that you are a just an objective observer who says the truth, which I think is very common among many, many academics.

Cameron Ghalambor 55:23

I agree, I think that's a something that we should think more about.

So, maybe we've been talking for a while, I'm gonna just hit you now that we've, we've just gotten very philosophical and everything. And, you know, I really appreciate your sort of thoughtful reflection on a lot of these questions. I guess my question, my last question to you is just like, looking forward, you know, you you just wrote this perspective, you know, Lande and Arnold, 40 years later. Where do you see things going into the future? What, you know, if we could go look at evolutionary biology inanother 40 years? Where, where do you see the trajectory? Is there a trajectory? Or and maybe you don't even need to go that far into the future. But I guess, you know, where do you see the field? What's the trajectory of the field right now? Where do you see like, interesting things happening?

Erik Svensson 56:46

I mean, a lot in our field has been very methodologically driven. I'm thinking of the genomic revolution and so on. But soon, almost every genome seems to have been sequenced, right? So what's happening now? I'm quite optimistic for whole organismal biology and evolutionary ecology. Because I think the low hanging fruit, the descriptive work on sequencing genome is over, we are entering the post-genomic era. It's interesting, we still don't understand phenotypes and how they evolved. In spite of having sequenced the genome, we explained very little of the phenotypes. This was also a disappointment in medicine, you know, the idea to have the human genome sequence and and you should have this personalized medicine, it has still not happened, right? The phenotype is still challenging, and there are many methodological problems to measure phenotypes.

If we are interested in traits and organisms, one challenge is simply logistical. How do we characterize and measure an organism in all its intricate details and correlations between parts? I would say in line with what David Houle in Florida have argued, we need a science of phenomics, we need phenomics after genomics. How can we accurately, fast and in a high throughput fashion, measure phenotypes better, and in a more objective way, to thereby study their evolution? That's a very methodological challenge.

But in two weeks, we will actually have a workshop here in my home university in Lunch, which one of my postdocs Moritz Lürig is organizing on how to use computer vision to extract meaningful phenotypic information from images. And I mean, in many of our labs, lab computers and on online digital databases, like Citizen Science databases, like a iNaturalist. There's a lot of interesting information about phenotypes, you can gather large amounts of data. I have a PhD student now who works on iNaturalist database. And she's collecting biogeographic study on damselflies with 100,000 individuals, you would never be able to collect that during you PhD. With this very efficient tool, like computer vision and machine learning, we can measure phenotypes in many, many different dimensions and much faster than before. So that's very much a technological advancement, and maybe as such not so interesting, but it can help us to do things more efficient, and maybe also give phenomics the place it deserves, as even more important than genomics. So I think that is one, maybe one way.

But then of course, there are many challenges is that, you know, logistically in evolutionary ecology, we would ideally like to study many populations to see. But we know, Cameron, you know how much work it is just to keep track of one population. That's why I gave up on birds. It was too much work to work, and then it was just one population. I don't know if we speculate if we would have small robots going out and collecting data. I'm not sure. That would take a lot of fun out of it, though, with the AI tools. They are amazing now in terms of identifying species. That's just the first step. But I set up my moth trap in my summer house, and I check in the morning and I just upload the photos. And I kind of I've been very bad with moths. I'm a birdwatcher, and I'm good at other insects, but moths are so difficult. But even I have learned them now.

Marty Martin 1:00:42

Wow. Well Erik, thank you so much. This has been a fantastic conversation. It's great to finally meet you in person and get to talk about your research and things. So hopefully, we can meet in actual physical person as opposed to just the virtual person. So before we wrap, we always give our guests you know, the chance to say anything that we didn't cover, was there something that you wanted to bring up that we didn't prompt you?

Erik Svensson 1:01:04

I think we have covered surprisingly much. Of course, we could have filled the whole podcast with damselflies. But that has to be the next one. I think, maybe I would like to say, and would be interesting to hear what you guys think about this, but I think there is an interesting tension in myself. On the one hand, you're thinking and doing theory and conceptual problem, on the other hand, I'm just a natural historian who like to be out there looking at bugs. And those two, I mean, ideally, they should. I mean, this is, I'm the same person, and they should, but ideally talk to each other. But sometimes I wonder, how much do you need one or the other? I mean, I admire theoreticians, like Mark or Patrick, for instance, who have no empirical research program, but I would have very big troubles in coming up with good ideas, if I didn't have some very concrete organism that I could relate to. What's your thoughts ?

Marty Martin 1:02:08

That's how I feel. I mean, I'm at heart a Natural Historian who uses modern molecular tools, but it's, it's. I guess, I am half a philosopher, I mean, I have as much but almost as much background in philosophy as I do in biology. So the question drive is as strong as just being out and observing natural variation. But yeah, I would never be able to be a pure theoretician, I still want to understand things that I just happen to like. Not very many people like how sparrows but but I do, and I'm perfectly happy to study them, because of them, they also are practically useful or useful in a more philosophical a conceptual sense, and that's great, but there's just an element of fun in it, too. What do you think, Cam?

Cameron Ghalambor 1:02:53

I think for me, it's interesting, because I guess, you know, to some degree, for those of us who are empirically oriented, we're, you know, our worldviews are shaped by the organisms and the, and the systems that we've worked on. And so you know, starting with birds, and then moving toward fish, and now insects and working in tropical environments, and temperate environments. You know, I've seen a lot of diversity. And then, you know, the theory helps me to interpret and kind of make sense of the variation, and maybe guides me in the interpretation, the questions, and sometimes that's self reinforcing. And my observations match my internal, you know, the you're saying the two parts of me, they talk nicely together, and then sometimes they're in conflict, because I have some preconceived notion, maybe based on theory, or what I've seen before about how things should be, and then I don't see it that way and then I have to somehow reconcile the two sides.

Erik Svensson 1:04:00

Yeah, that's interesting, because that leads us into bias. How, like, some years ago there was this about tropical bias in AmErikan Naturalist, the theme issue by Marlene Zuk and colleagues, I think that our we have the temperate bias in a lot of, of our theories and ecological and evolutionary theory is most well known is perhaps, you know, the evolution of bird clutch size that that at higher latitudes, it's the clutch size is limited by food, David lack,

Cameron Ghalambor 1:04:30

I was obsessed with that idea. And as a graduate student.

Marty Martin 1:04:33

Yeah, we were all obsessed by that at some point.

Erik Svensson 1:04:38

No, but I also have things I've been thinking a lot about in terms of insects and sexual selection and particular sexual conflict that up here in the North, we have these short explosive summers with a lot of individuals and much more antagonistic interactions. Male mating harassment of females which are crucial to maintain these female polymorphous were studying through sexual conflict. But if we go to the tropics, the densities are much lower. So this is kind of density dependent and antagonistic interaction or prosumer, much weaker general trend the density density bias. So I think this is kind of our natural history background can both help us but also hinder us from seeing things.

Marty Martin 1:05:35

Yep. Good. Well, thank you so much, Erik. It's been a lot of fun. We'll do it again soon and do only damselflies next time.

Erik Svensson 1:05:43

Thanks a lot!

Marty Martin 1:05:54

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Cameron Ghalambor 1:06:04

Thanks to Steve Lane, who manages the website and new producer Molly Magid for producing the episode

Marty Martin 1:06:10

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Marty Martin 1:06:22

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