FRANCISCO J. AYALA: TESTING HIS IDEAS ON BIOLOGICAL PROGRESS

Francisco J. Ayala: Investigando sus ideas sobre el progreso biológico

Andrés Moya
Professor of Genetics, University of Valencia
andres.moya@uv.es; https://orcid.org/0000-0002-2867-1119

Amparo Latorre
Professor of Genetics, University of Valencia
amparo.latorre@uv.es; https://orcid.org/0000-0002-9146-7284

ABSTRACT: Francisco J. Ayala was one of the great scholars of progress in biological evolution. For Ayala, progress consists of a net directional change in some characteristic that improves the descendants in a given lineage relative to the ancestors. This is an axiological proposal, but not at all unscientific. The traits are objective properties that can be measured in individuals, populations, or species and, ultimately, the entire evolutionary tree. Here, we develop Ayala's ideas about progress and propose that the trait where the trend can be contrasted is probably the complexity of genomes. We also consider the need to apply statistical tests to determine whether trends, if they exist, are passive products of evolution from the simplest to the most complex or whether, on the contrary, there is directionality or a process driven, among other things, by natural selection.
KEYWORDS: progress, biological complexity, genome complexity, evolutionary trend, complexity metrics, symbiosis, regressive evolution.

RESUMEN: Francisco J. Ayala ha sido uno de los grandes estudiosos del progreso en la evolución biológica. Para Ayala el progreso consiste en un cambio direccional neto en alguna característica que mejora, en un linaje dado, a los descendientes con respecto a los ancestros. Se trata de una propuesta axiológica, pero en modo alguno no científica, porque esas características son propiedades objetivas que podrían medirse en los individuos, las poblaciones o las especies y, en última instancia, en todo el árbol de la evolución. Aquí desarrollamos las ideas de Ayala en torno al progreso y proponemos que esa característica donde se puede contrastar la tendencia es la complejidad de los genomas. También

consideramos la necesidad de aplicar pruebas estadísticas para determinar si, en efecto, las tendencias, de existir, son productos pasivos de la evolución desde lo más simple a lo más complejo o, por el contrario, existe direccionalidad o proceso dirigido, entre otros, por la selección natural

PALABRAS CLAVE: progreso, complejidad biológica, complejidad del genoma, tendencia evolutiva, métricas de complejidad, simbiosis, evolución regresiva.

1. EVOLUTIONARY PROGRESS: A LONG DEBATE

A persistent display of biodiversity characterizes life on planet Earth. If we examine the geological record of species that have appeared, we usually find an increase in species over time. This statement does not contradict the finding of major extinctions that have occurred at certain times. It is also true and often debated that if we consider the record not in terms of the number of species but in terms of large taxonomic groups, the phyla, it seems that there was a particular moment in the Cambrian when a large number of them appeared and that after that there were virtually no new ones. In any case, life has a tenacious persistence to proliferate and differentiate into species. After some large taxonomic groups are extinct, life evolves from the surviving species.

The basic idea explaining this process of life diversification is Darwin's theory of evolution by natural selection. The theory is based on the filiation between species so that some are the product of others from which they descend, thus configuring the Tree of Life. This is the other outstanding contribution of the theory (Sober, 2009).

One question remains unclear when considering the evolution of life on Earth over four billion years to give a round number. It is the question of the complexity of living beings. Prokaryotes have evolved since the origin of life, for more than three and a half billion years, until the appearance of unicellular eukaryotes, then multicellular eukaryotes, and within these, taxa with progressively more sophisticated cellular organizations. This is not to say that prokaryotes have not evolved; quite the contrary. If we were to characterize the planet's biodiversity today, the most diverse and abundant organisms would be bacteria and archaea. We leave aside the case of viruses because they are not autonomous agents since they depend on both prokaryotic and eukaryotic hosts. However, if we were to include them, we would also have to point out that their diversity is an order of magnitude greater than that of bacteria. In any case, and speaking of complexity, eukaryotes are also com-

plex organisms. However, they represent a much smaller number of species, biodiversity, and biomass than their prokaryotic relatives, including viruses.

Some well-known authors of evolutionism, starting with Darwin himself, admit that there is progress in evolution. This is the case of Julian Huxley, Richard Dawkins, Simon Conway Morris, and Francisco Ayala. Others like John B.S. Haldane or Stephen J. Gould are notorious deniers. This difference in thought is surprising, to say the least, since they are all evolutionists. Thus, giving different weight to natural selection as the driving force of the evolutionary process, they enter the debate on evolution's existence or lack of progress. A weighty question underlying the debate is whether this progress, if it exists, entails a certain inevitability in the appearance of more complex entities. Well-known is Gould's (1996) argument that if the tape of life on Earth were replayed, it would not resemble what has happened on our planet. Gould does not deny that complexity seems inevitable and passive from something simpler. But he doubly denies that this complexity could be the product of natural selection (which would be a guiding or driving force) and that such complexity could be repeatable because of evolutionary novelty's contingency or random nature. However, the answer is not as simple as it may seem, and frankly, it remains a profound question with many implications in fields beyond biological evolution itself (Moya, 2015, 2017).

2. AYALA AND BIOLOGICAL PROGRESS

In a famous text, which can be considered one of the first texts to develop the new specialized branch of the philosophy of science, the philosophy of biology, whose editors were Ayala and Dobzhansky (1974), Ayala wrote a chapter on the subject of progress in evolution (Ayala, 1974). With the rigor that has always characterized him and the broad intellectual training he has enjoyed, he first considers the concept of progress in biological evolution. He believes the term implies an axiological consideration: progress implies a tendency in which older biological entities are worse than newer ones that have evolved. Better or worse, however, is not equivalent to good or bad, which would imply more moral terms. One can be better or worse at something without this implying goodness or badness. This consideration of Ayala's is important because he does not deny that there are values in the question of progress—hence axiology—but we cannot think these values are exclusively those proper to morality. In this study, Ayala deals with other related ques-

tions about whether this tendency can be sustained and whether there can be cases of non-progressive evolution.

The issues that Ayala addressed in his 1974 study are developed again and in greater detail in a paper he published in 1982 in the Spanish journal Arbor (Ayala, 1982). We will develop this last study here because Ayala includes considerations on the new science of genomics, which was in its beginnings. Thus, this text can be considered quite seminal regarding Ayala's progress, which he treated with a certain systematicity in subsequent studies (Ayala, 1988, 2017).

Comparison with other concepts

Ayala points out that "progress" has similarities with "change," "evolution," or "direction or trend," but they are not identical. A "change" implies a change, but although progress implies change, not all biological changes are progressive. The same is true of the term "evolution," for evolutionary changes are not necessarily progressive but imply prolonged change. In addition, his third comparison is with "direction or trend. Evolutionary trends are directional changes, but for that trend to be progressive, there must be an improvement of something—important, not an improvement "toward something," but we repeat, of something. Therefore, progress implies directional change, but directional change does not necessarily imply progress.

Definition of progress

For Ayala, "progress" is the systematic change of a characteristic present in all components (taxa) of an evolutionary sequence, such that the most recent taxa show an improvement over the preceding taxa. Very synthetically, progress would be a directional change for the better of a given trait. However, as noted above, "for the better" does not necessarily imply goodness or badness. So, what kind of traits are we talking about? Ayala mentions three possible qualities. Better could be "more efficient," "more abundant," or "more complex. Considering an evolutionary sequence of biological entities over time, we can point out that these three characteristics would indicate progress if they increased over time. Another question is the possibility of measuring them, mainly when the sequences correspond to geological

times, millions of years. Let us look briefly at what we can expect from these three metrics of evolutionary progress.

Three measures of progress

Efficiency equals greater biological fitness, but whose? In terms of changes in the genetic structure of populations, individuals with greater biological efficiency populate them with their offspring over time than individuals with lower biological efficiency. However, by the nature of natural selection, this population trend depends on the environment, with those who produce relatively more offspring being more efficient. Nevertheless, environmental conditions can vary, which is quite possible when talking about long time intervals, not just a few generations but millions of years. Here, we have to consider whether the continuous action of natural selection, always favoring some individuals over others, systematically increases the average efficiency of populations. Note that we are not talking about one individual being universally more efficient than another. Depending on environmental factors, individuals can change their efficiencies, and whoever was more efficient at one time may no longer be so for any other.

On the other hand, although we can consider this characteristic conceptually important, it is difficult to determine the metric empirically since comparing the increase in efficiency between taxa in the series that are far apart in time is difficult. However, it is worth keeping this in mind because it has often been criticized that selection cannot be behind a sustained evolutionary trend. After all, the environmental conditions under which the taxa in the series evolve will change. Let us look at it from the perspective not of specific individuals and their descendants but of populations. The issue takes on a different dimension, with natural selection as an explanatory mechanism for the directional trend and improvement of populations and species over time. Darwin and Julian Huxley saw natural selection as an engine for the progress of species, for their improvement, and ultimately for more recently derived species to be more efficient than their phylogenetic ancestors.

Abundance may be a second metric. This metric presents a similar difficulty to biological efficiency over significant time scales. But for Ayala, returning to the conceptual realm, abundance, in this case, the number of species or individuals of each species, could be another metric of biological progress. The greater the number of species, the greater the possibility of creating new environments for new species to explore. If we could measure (actually

count) the number of individuals of species over time, or the number of species, or even more generally measure the mass of all living things (biomass), abundance, so understood, could be an indicator of progress if it could be shown to increase over time.

The third metric to which Ayala refers is that of complexity. It is a metric with many edges, beginning with its definition and eventual measurement. Nevertheless, and as we indicated in the introduction, there is a certain conviction in the evolutionist community that complexity grows with evolution, regardless of whether what might be driving it is natural selection or, to go to the other extreme, whether it is something inevitable because what can be expected in the evolution of life, which began with few complex entities, is that their descendants will become more complex.

In this environment on the metric of complexity, Ayala takes a step forward and considers that a possible criterion of progress could be that of the increase in the amount of genetic information of organisms and that those living today present, on average, a more significant amount of genetic information than that of the ancestors from which they come. However, he acknowledges (the paper is from 1982) that an enormous difficulty with this metric is that there is no way to measure the amount of genetic information in the DNA of organisms. Moreover, Ayala believes that the amount of information is not necessarily the amount of DNA but that the "complexity" of an organism could be approximated in this way. He does what any scientist would do: try to find a way to approximate complexity by measuring it with the techniques available at the time.

3. COMPLEXITY

As we have noted, the question of complexity in biological evolution is recurring. Adami (2002) has already stated that "whether or not complexity increases in evolution is one of the central questions of evolutionary biology." We can agree with him, but defining complexity is complex and challenging because we can have many approaches to the concept. Complexity refers to the structure or function of organisms or species or the information involved in their construction, development, or functioning. Without claiming to be exhaustive, we can speak of four significant types of complexity: structural, functional, hierarchical, or physical.

Structural complexity could be considered regarding the number of structural types that comprise individuals. The underlying idea is that of "parts." In a simple notion of complexity, the organism with more parts is more complex. But, of course, "part" is a somewhat ambiguous term. Parts could be many types of cells, tissues, organs, etc. More complex would be those species whose individuals have more of these types of parts. Something similar could be said of functional complexity. How many functions can an organism perform? This is a rather tricky question to answer. However, conceptually, if it could be counted, we would say that the organism that can perform more functions is more complex. In the same way, we could consider complexity based on hierarchization. For example, to put it simply, considering that organisms have cells that are organized into tissues, tissues into organs, and organs into apparatuses, the degree of control of the higher levels of the hierarchy of function over the lower ones and some of the lower ones over the higher ones, all of this configures a degree of complexity such that those species with higher levels of such hierarchization would be more complex than others with lower levels of the same.

As soon as we think about these three possible complexity metrics, we can appreciate the enormous difficulty in finding a universal measure of complexity based on structural, functional, or hierarchical considerations when considering the taxa of the Tree of Life. Then, of course, the possible detection of evolutionary trends and the values of the metrics are higher in more recent taxa. An excellent fundamental study on this issue of complexity based on the number of parts and their differentiation was developed by McShea and Brandon (2010), where the authors argue that it is a universal natural tendency in evolution to observe a process towards greater biodiversity and complexity.

4. **PHYSICAL COMPLEXITY**

A fourth measure of complexity is physical complexity (Adami, 2002). It is nothing more than an evaluation of the amount of information in a population of genomes. Adami's proposal is a measure that calculates the amount of information based on Shannon's classical definition. Those nucleotide sites in the genomes occupied by the same type of nucleotide most likely show the effect natural selection has had on the individual carrying that nucleotide in that position. A mutational change to a different nucleotide would typically be selected against, and that organism would have less biological fitness.

There could also be, though less likely, a new mutation that would imply greater efficacy in the individual carrier. The tendency would then be for that new nucleotide at that site to spread to the offspring population over time.

On the other hand, we would have sites with a more or less equiprobable frequency of nucleotides in the genome population. The situation can be interpreted to mean that these sites are not so discriminated by natural selection, and the tendency would be, as indicated, for these sites to be much more variable or polymorphic than the sites under selection. The information measure would be the sum of the information detected for each site in the genome population.

There have been similar proposals for measuring information in genomes at the population level. There is a precedent before Ayala (1982) in Kimura (1962), the father of the neutral theory of molecular evolution, who also used measures based on Shannon information applied to population genetics. This measure of the information in genomes is commonly called a measure of physical complexity. The availability of the nucleotide sequence of genomes has opened the field to determining complexity based on genomes. This was impossible in Kimura's time, Ayala's 1982 paper, or Adami's early work a few years later. Genomics emerged as a major science of biology after the work of these and a few other authors. It is essential to note this circumstance because, compared to the other metrics we have discussed, physical complexity has the tremendous empirical advantage of being measurable and comparable. Organisms have their genomes, and genomes in populations and species can be determined.

A good complexity metric should meet three requirements: precise definition, empirical measurement, and universality. The definition is a problematic issue, as we have already seen that it leads to possible types, but having conceptually understandable definitions is important for advancing the study of complexity. The types of complexity outlined here, including physical complexity, are possible definitions. The following property is a possible empirical measure. This property is highly desirable for advancing the demonstration of complexity evolution and progress trends. Despite their conceptual clarity, some types of complexity mentioned above have many measurement problems. How do we determine the number of parts or functions of an organism? We are not suggesting that this cannot be approximated, but it is challenging. Finally, we have universality. This property is relevant for comparative purposes: the complexity metric must be feasible or exist in any organism on the Tree of Life. The genome, and any metric we propose for it, has all three properties.

It is possible to criticize the genome complexity metric(s) as reductionist because they ignore many potential sources of complexity that are largely ignored by the other complexity metrics under consideration. In this light, one could accept that any complexity in genomes would be a poor indication of the true complexity of the organism or species. This criticism cannot be ignored, but we can also think of the genome as a historical record of the evolution of organisms. The events a particular lineage went through to become the species it is today are somehow recorded in its genome. It is true, one might think, that other things are not recorded, and here we would debate whether any metric of complexity in the genome is a good indicator of the overall complexity of the organism.

5. COMPLEXITY METRICS IN INDIVIDUAL ORGANISMS

Returning to the seminal work of Ayala (1982), it should be noted that he proposes an idea for the metric of genome complexity that we believe is superior to that of Adami (2002). As we have commented, this author proposes a population measure of genome complexity. A population is needed to obtain the value of the metric. This makes comparative studies difficult, especially when phylogenetically distant species are considered. Let us say that this approach has a specific problem of empirical measurement. However, Ayala proposes a measure, which he cannot specify at this time due to the nascent state of genomics, that directly considers the individual organism. A measure of the population could be given by resorting to the mean values or some other statistic of the metrics of the organisms that make up the population.

As a result, many physical complexity metrics are already measured directly on the genomes of individual organisms. This is not the place to develop them in detail (the interested reader can consult Moya et al., 2020; de la Fuente et al., 2023). There are metrics based on the possible compression of genomes, the analysis of the distribution of k-mers (nucleotide segments of a given length), compositional segmentation, or the study of the periodicity of genomes, to name a few. Most of these metrics try to derive a measure of information by comparing an actual genome with a random genome of the same length and are closely related to how much entropy exists in genomes and how much anti-entropy and from the relationship between the two derive a measure of information indicative of their complexity.

6. **EVOLUTIONARY TRENDS IN PHYSICAL COMPLEXITY**

Armed with some of these metrics, we can now evaluate possible trends in the evolution of complexity and consider whether there is evidence of progress, as Ayala defined it. It is a research program, but the seminal idea is to see if we have evidence that physical complexity is more remarkable in different lineages when more recent organisms within them show greater complexity than older ones. It is also worth considering formulating the confirmation of the eventual trend for the entire Tree of Life. In this regard, Ayala introduces two other very pertinent terms: what he calls "uniform progress" and "net progress." In the former, one would observe a systematic increase in the metric, while in the latter, one would not necessarily observe a systematic increase; however, when examined as a whole, one would observe that older members of the lineage would have lower values than more recent members and that the overall result would be an increase. Ayala is aware that observing downward variations in a metric, or even no variation for a given period, is common in biological evolution. But this would not contradict the notion of net progress.

It is also fully aware of what we might call regressive evolution, uniform or net trends, but of the loss of complexity and progress. We have been working on the case of evolutionary regression of bacteria living in endosymbiosis with their eukaryotic hosts. Endosymbiosis is the intracellular life of bacteria inside other organisms. We observe that these bacteria reduce and degrade their genomes, losing autonomy and independence as autonomous entities that are free-living bacteria from which they evolved (Latorre and Manzano-Marín, 2017). Endosymbiosis is a particular form of regressive evolution, but to a certain extent, because the fact is that the eukaryotic host evolves with these bacteria and forms a new entity, in principle, more complex than if we consider the host without this type of microorganisms. The important role of symbiosis in the origin of the eukaryotic cell itself is well known (Margulis, 1981).

We are just beginning to see evidence for the evolution of physical complexity in different lineages of evolution. In a recent study, we examined the increase in genomic complexity of cyanobacteria, a group of very ancient bacteria that has given rise to increasingly complex lineages in terms of the complexity we have measured (Moya et al., 2020). In this study, we applied some of the metrics mentioned above. We found, in the case of some of them, and with sufficient statistical consistency, that more recent taxa had a higher value of these metrics than older ones. It is interesting to note that by

applying phylogenetic inference methods, we may be able to estimate what the value of the complexity metrics of the ancestors whose genome is not available might be now.

We mentioned the issue of statistical consistency of trends. This is a very important issue. Ayala formulates his definitions of net or uniform progress and does not explicitly mention the need for statistical testing of trends. However, there are well-developed procedures for obtaining meaningful statistical evidence of trend values, especially in paleontology. In this regard, Gould (1966) extensively analyzes this issue of statistical testing to return to the charge about any trend in evolution, especially that which might exist for the entire Tree of Life.

For Gould, evolution from the simplest to the most complex is a passive product of evolution, which is to be expected given that there is a wall to the left of evolution imposed by the most elementary forms of life, the first microorganisms. From there, we can only expect evolution to grow in complexity without direction. Passive is an important word, indicating the opposite of "driven directionality." But, who could direct an evolutionary trend toward greater complexity? Gould himself, following other authors (most notably McShea) who had worked on evolutionary trends in macroevolution, formulated a series of tests of a statistical nature to examine whether the trends could be a possible undirected inertial product of life itself once it appeared on the planet, or whether, on the contrary, we had tangible evidence that the trends were directed, by natural selection. In our work (Moya et al., 2020), we take the above statistical tests very much into account to confirm whether or not there is evidence of a directed trend in the evolution of genomic (physical) complexity in cyanobacteria, and we find, as already indicated, that some of the metrics show it.

As Ayala noted, we cannot believe that the trends—in our case, toward increasing physical complexity—are not a universal constant, neither uniform nor net. There are many evolutionary trends; we have already mentioned endosymbiosis, which can be considered a regressive trend, as well as the evolution of parasitism, a widespread phenomenon in biological evolution. However, the critical question remains: is it possible to think of general evolution as a process of net incremental progress in physical complexity? In the case of Gould, an ardent critic of this issue, we do not believe he has resolved the question. Curiously, he notes that if life today is characterized by anything, it is by the extraordinary diversity of microbial life, such as the number of species, individuals, or biomass represented by the eukaryotic life of multicellular organisms. In this sense, Gould argues, we should say that life has

not evolved toward greater complexity since the primitive prokaryotes that first appeared are the ones that have persisted, evolved, and diversified the most. Nevertheless, this argument is not enough. The question is whether the biological entities that have appeared in evolution are progressively more complex. Our approach asks whether the most recent entities exhibit greater physical complexity in any metrics we consider measuring.

7. **IN CONCLUSION**

The question of progress, reconsidered here from the perspective of the evolution of complexity, particularly the physical complexity of genomes by any metric that measures such complexity, remains open. Indeed, the question remains a significant challenge in the study of biological evolution, beyond whether it is presented to us as evident, which it is not, that evolution toward greater complexity is a fact of evolution. We do not know, but we may not have been able to prove it.

Acknowledgments

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El regalo de Darwin a la ciencia y a la religión

Francisco J. Ayala

¿Es posible creer en Dios y aceptar la evolución? ¿Qué nos dice la ciencia sobre el origen y la diversidad de la vida? ¿Qué nos dice la religión sobre el sentido y el destino de la vida? Estas son algunas de las preguntas que aborda Francisco J. Ayala en su libro póstumo "El regalo de Darwin a la ciencia y a la religión". Ayala ha sido uno de los más prestigiosos investigadores internacionales de las últimas décadas en el campo de la Biología, que ha dedicado su vida al estudio de la evolución y al diálogo entre ciencia y fe. En esta obra, ofrece una visión lúcida y rigurosa de la biología evolutiva y de sus implicaciones filosóficas y teológicas, mostrando que la evolución no es una amenaza para la religión, sino una oportunidad de enriquecimiento mutuo. A lo largo de toda su reflexión lanza una invitación a contemplar la obra de Dios en la naturaleza y a reconocer su presencia en la historia. Propone una lectura crítica y creativa de las Escrituras y de la tradición cristiana, animando al lector a vivir su fe con coherencia y responsabilidad. El libro de Ayala es un regalo para todos los que buscan una comprensión más profunda y armoniosa de la realidad.
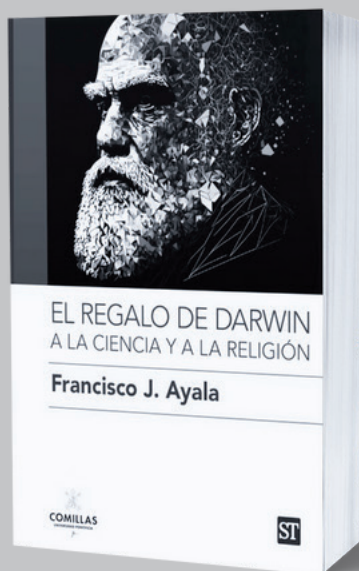
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