ON THE MEANING OF NATURAL

SELECTION*

Rafael Andrés Alemañ Berenguer†

Summary: Natural selection is one of the fundamental keys of evolutionary biology, which is as much as saying of almost all life sciences. However, the effort to assess its true meaning has been involved in endless controversies almost from the beginning. The

rethinking of natural selection through an abstract scheme with three ingredients -

-population, environment and interaction between them- could significantly contribute to

clarify this debate.

Keywords: Natural selection, evolution, darwinism, population, biosystems.

1. Introduction

Since it entered the scientific vocabulary sponsored by the famous Charles Darwin,

around the concept of "natural selection" there always raged a gale of controversies, disputes

and qualifications (Bowler 2003). Such entanglements did not prevent the expression from

jumping the barriers of a strictly biological use to finally root in fields as diverse as

economics, cosmology or epistemology (Sammut-Bonnici & Wensley 2002, Von Sydow

2012). Under the distorted motto of "the survival of the fittest," Herbert Spencer and the

social Darwinists used it to justify the social classism of their times. Lee Smolin appealed to

it to rule out those universes that do not meet certain conditions of viability in his "fertile

universes" cosmology. And Karl Popper -very reluctant in the beginning on the logical

content of natural selection—used this idea to justify the triumph of some scientific theories

in explanatory competition with others. And even, with much less formality, there are some

Darwin Awards to highlight that the deaths of some individuals caused by their incredible

clumsiness, expose in themselves the macabre enforceability of natural selection.

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https://philpeople.org/profiles/rafael-andres-aleman-berenguer

Without abandoning the field of biology itself, the lively debates about the genuine meaning of this concept glimpsed the historical development of evolutionary theory and served as a dialectical weapon of convenience for creationists. Is natural selection (NS from now on) a mechanism?, and if so, how to classify and elucidate its operation? What does the "survival of the fittest" (or the "strongest" in its grossest version) mean? Is the SN a "force" (Sober 1984) in the sense that this term has in Newton's mechanics, for example? What is the explanatory scope of the NS?

In a letter to the famous geologist Charles Lyell, dated June 6, 1860, Darwin himself expressed his reservations about the relevance of such an expression (Burkhardt et al 1993, p. 243):

"(...). I suppose "natural selection" was bad term; but to change it now, I think, would make confusion worse confounded. Nor can I think of better; "Natural preservation" would not imply a preservation of particular varieties & would seem a truism; & would not bring man's & nature's selection under one point of view. I can only hope by reiterated explanations finally to make matter clearer."

The reflections of the celebrated English naturalist on the misunderstandings generated around the SN will justify our brief incursion on the trail of its meaning. To this purpose, we will enquire whether the SN is part of a larger group of processes with which it shares some distinctive features and, if so, the features that characterize the content of the SN itself within that family of processes.

2. What is "Natural Selection"?

Scientific theories are not born full-fledged in the minds of researchers, as Athena emerged from the head of Zeus. There is always a stammering stage in which the concepts are diffuse and many edges remain to be polished, as happened with Darwinian evolution (Fisher 1930, Haldane 1957, Berstein *et al* 1983, Endler 1986, Williams 1992, Graham 2008). The criticisms harvested since its inception by the idea of SN, generally based on faulty interpretations, were answered by Darwin in later editions of his seminal work, *The Origin of Species* (Darwin 1920, p. 114):

"Several authors have misunderstood or objected to the term natural selection. Some have even imagined that natural selection produces variability, and thus implies only the conservation of the varieties that appear and are beneficial in their living conditions. (...) In the literal sense of the word, undoubtedly, natural selection is a false expression; but who will never raise objections to the chemists who speak of the elective affinities of the different elements? (...) It has been said that I speak of natural selection as an active power or divinity; But who charges an author who talks about the attraction of gravity as if regulating the movements of the planets? We all know what is understood and imply such metaphorical expressions, which are almost necessary for brevity. Similarly, it is also difficult to avoid personifying the word Nature; but by Nature I mean only the total action and result of many natural laws, and by laws, the succession of facts, insofar as they are known for sure by us. Getting a little familiar, these superficial objections will be forgotten."

Indeed, even by adding the adjective "natural", the word "selection" itself implies powerful evocations of the artificial selection practiced by human beings in countless activities. The farmers who decide at their convenience the reproduction of certain cattle, the breeder who crosses certain dog races to create others, or the farmer who separates the straw from the wheat, they all select in one way or another. And why should we stay within the nature domain? It is commonly discussed on the selection of candidates for a job, the selection of papers to be published in a magazine, or the selection of expedients to be processed in order of priority. Any discrimination between the elements of a set on the basis of certain established criteria constitutes in itself a selection activity.

Undoubtedly, Darwin did not refer to that choice among various options, let alone made by an active agent, when issuing the concept of SN. His thoughts pointed to something deeper with profiles less easy to specify. It is well known that he said he was inspired by the demographer Thomas Malthus, who regarded the struggle for existence of individuals whose number was growing in an environment of insufficient resources as inevitable. By moving that conflict to the realm of wild nature, it is how Darwin enlightened the notion of SN, one of those great ideas, dazzling in its simplicity, which amazes us by the fact that no one had thought of it so clearly before. So fascinating as it is, SN inspires words of admiration even among those who doubt their omnipotence (Arana 2014, pp. 81–82):

"(...). It is something so simple, so obvious and so natural that you have no choice but to occur in reality. (...) It is almost an *a priori* truth: it cannot fail if we accept the principle of contradiction. Its argumentative skeleton could be summarized as follows: *Random inheritable variations* + *survival of the fittest* = *growing and diversified adaptation*. It is a formula that sounds more like a deductive equation than an empirical generalization. Let us add temporary episodes of geographical separation and the incubation of new species where there was once only one will become obvious. As long as new variations continue to emerge and nothing hinders the free competition of the living beings, evolution is guaranteed. (...)."

In more detail, one of the founders of neo-Darwinism reproduces Darwin's explanatory model (Mayr 1992, p. 86) as a two-step deductive chain. It is initially based on three assumptions:

- (A1) the limitation of natural resources in any finite environment,
- (A2) the super-fecundity (potentially unlimited growth) of populations of living beings,
- (A3) the observed stability of existing populations.

From these three premises it follows that there must be competition among individuals in a population to obtain the resources without which they cannot subsist. This conclusion, in the second stage of reasoning, is taken as a premise (B1) along with two others:

- (B2) the appearance of certain phenotypic variations in individuals of the same species,
- (B3) the inheritance of the largest part of that variability to the subsequent generations.

Resting on these three statements the second and definitive inference is deduced, which is finally the differential survival —or "natural selection"— of individuals carrying certain characters. This phenomenon, repeated in the very long term, will lead to the evolution of species. Other more elaborate exposures analyze the theoretical presuppositions with greater refinement (Moya 2003), but the plot skeleton happens to be the same.

The questions that spurred us at the beginning arise again even more challenging. What makes the analogies with the SN so versatile to captivate us with the force of a seemingly inexorable logic? And what is truly distinctive about the SN compared to other similar processes? If we need a firm basis for comparison, perhaps we should turn our considerations to the phenomena of the inanimate world in search of an answer to these disturbing questions.

3. Systems, surroundings and interactions

Imagine a volume of gas, in sufficient quantity to apply statistical methods, whose molecular size is characterized by the parameter r. Such a gaseous volume is located in one of the two sections of a container; these two sections are separated by a filter. The size of the pores of that filter, in turn, is given by the value R. As we can infer, after a certain time on the other side of the filter a molecular population will appear whose size r is equal to, or less than, R.

If we assume that the molecules that pass through the filter are definitively removed, so that they cannot go back through their pores in the opposite direction by mere random motion, what will the distribution of molecular sizes in the remaining gas be? It could be said that all those molecules would be larger than the pore size, $r \ge R$. But it has not necessarily to be this way unless we wait for an infinite time. There may remain molecules with $r \le R$ if the angle with which they impacted on the pores does not allow them to cross to the other side of the filter.

Constructing a function f that contains information on that characteristic, as well as the number and size of the pores of the filter (assuming random distributions), from the initial number N of molecules, the fraction that will remain without crossing the filter will be given by the product Nf. The point to highlight now is that the amount N will always be less than the initial population N. The discrimination occurred in terms of the molecular size has reduced the number of the original population.

No matter if we refine the proposed example a little more. Let us assume a barrier of potential V and some elementary particles able to cross it by the quantum-tunnel effect characterized by the N(E) function, which gives us the number of particles that have a certain energy value. Although we can calculate the probability of passage of each individual particle based on its energy, when launching a flow of particles against the barrier it is not statistically difficult to obtain the distribution of energies for those ones that manage to overcome the obstacle. Again, the number of surviving particles will be lower than the original quantity before the interaction with the potential barrier.

However trivial they may seem, the preceding examples capture the essential aspects of those processes that we could call "differential survival" or also "environmental interactive screening". It is really a repeated pattern in all fields of research on nature (Fernando and Rowe 2007, Blume-Kohout and Zurek 2008). We have, at an initial moment,

a set of elements K, environmental features S that will interact with the elements of K, and the material process I that substantiates that interaction between K and S. Among other words, in the triad $\langle K, I, S \rangle$, the interaction I acts as the filter, or screen, that discriminates between the elements of the initial set K to give rise to another set of elements K', whose cardinal is smaller than the initial (fig.1).

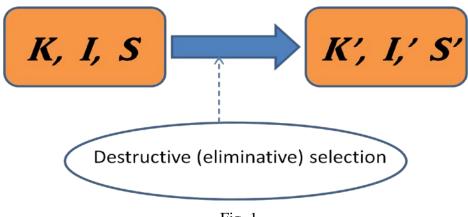


Fig. 1

Let us reflect for a moment on that screen *I*, which acts in a semi-stochastic manner. In fact, the motion of the molecules that pass through the filter pores is not purely random —as a shaken ideal dice would be—but based on their size and spatial direction. We have a causal link between the passage of molecules through the filter and these two physical characteristics. But it is also true that we cannot predict the concrete molecule that will pass through the filter at any time due to the peculiarities of the statistical mechanics that govern these systems. That is the random aspect that is essential to put forwards in this class of phenomena. And that is why those phenomena can be called semi-stochastic (partially causal and partially random).

On the other hand, nobody will be surprised by the fact that the molecules larger than the pore diameter fail in their attempt to cross it, nor will we be astonished that the quantum particles that cross a potential barrier meet the statistical expectations of quantum theory. Interactions express the response of material systems to the dynamic conditions of their environment under the natural laws that govern them. That is why we do not worry when the electric charges in the presence of a magnetic field are diverted in different directions according to their sign. Because that is exactly one of the behaviors that characterizes them as such electric charges, and no one would try to argue that the laws of electromagnetism are empty tautologies.

4. Natural selection as a dynamics of environmental screening

Let us return to the scientific field in which we began, biology, to consider the possible applications of the preceding arguments. It seems obvious that, in the Darwinian sense, K would be a population of living organisms, S would represent the demands of the environment (finitude of resources, competition between members of that same population and others, environmental changes, etc.) and I would symbolize the interactions between the elements of K and the challenges of the ecosystem.

For the sake of simplicity, let us imagine a population of foxes that, as good hare predators, depend on their hunting skills to survive. This is a very simplifying example, no doubt, but it will serve our immediate purposes. Compared to the gas filter, instead of molecules we will now have foxes as elements of K, the critical parameter will be here the speed (of chasing prey) and not the molecular size, S will include the availability of prey and I will refer to the prey-predatory interaction between hares and foxes. Since I will include, in general, a multitude of other variables beyond mere speed, variables that are in turn dependent on the specific characteristics of every ecosystem (Lande and Arnold 1983), it could be referred to as "ecosystem screening".

Just as it is not surprising that —in strict obedience to the laws of statistical mechanics— only molecules with a size equal to or smaller than the diameter of the pores pass through the filter, it should also not surprise us that the fastest foxes —obeying the laws of kinematics— successfully overcome the slowest predators. And therefore, as a result of the finite number of prey, only the fastest foxes will feed themselves and survive, as the rules of metabolism biology (and ultimately the thermodynamic laws) establish.

If this is, in summary, the factual content of the exceedingly repeated phrase "survival of the fittest," why do so many people regard it as a hollow tautology? The answer could lie in the difference between the simple physical models usually taken as an example - molecules of a gas passing through a filter, particles charged in an electromagnetic field, etc.— and the complexity inherent in the vast majority of biological systems. While a handful of properties (energy, diameter, electrical charge) is enough to analyze the behavior of interest, models of biosystems tend to be enormously more complicated by relying on multiple variables that also interact with one another in not very well known ways. That is why it is summarized by saying "the fittest survive" instead of "those who have such traits survive," and having taken that step it is almost irresistible to fall —confusing causes and

effects— in the circular reasoning mentioned above: "the survivors are the fittest" and "the fittest are those who survive".

For the purposes of the previous reasoning, we should not think that populations of living beings are comparable to the molecules of a gas, for the simple reason that in the first case the elements of K have the ability to reproduce and generate new members of the set with characteristics not always identical to their predecessors. Certainly the molecules or elementary particles lack properties such as reproductive variability, and that is one of the reasons responsible for the particular specificity of biosystems. Otherwise in subsequent iteration we would pass from K to K' and then to K'' with a ever-decreasing population until the total extinction of its components. What actually happens is that from the first triad $\langle K, I, S \rangle$ we move on to another $\langle K', I', S' \rangle$ in which both the conditions of the S' environment and the ecosystem screen may have changed, as well as the interaction I' derived from them.

Now we can see with a better perspective the ambiguity of an expression as "natural selection". Because anyone of the following instances could be called NS:

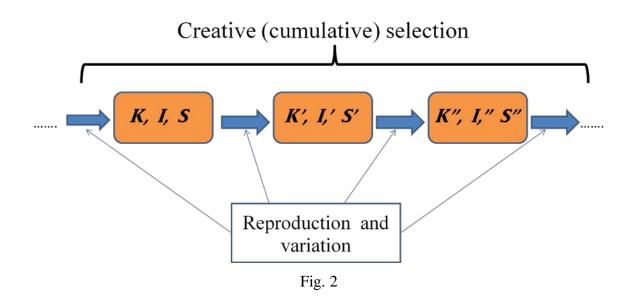
 (1^{st}) The mere replacement of the population K by K'. The NS thus contemplated would be the effect, and not the cause, of the change in the characteristics of a population over time.

(2nd) The transition from a triad $\langle K, I, S \rangle$ to the next one $\langle K', I', S' \rangle$. Here we adopt a broader point of view and we do not only consider the passage from K to K', but also the other components of the list that make it possible: the S ecosystem and its interactions I with the members of K.

(3rd) The series of *n* transitions over a certain period of time that takes us from the triad $\langle K, I, S \rangle$ to $\langle K_n, I_n, S_n \rangle$. Now our perspective is even broader, because the higher the number *n*, the greater the transformation of the members of the initial population; that is, the evolutionary process will manifest itself more clearly.

It is important to notice that if we consider a single transition (the passage from $\langle K, I, S \rangle$ to $\langle K', I', S' \rangle$, for example), the ecosystem screening will only result in a suppression of the elements that do not meet the conditions imposed by I, as stated in the previous section. Thus, the NS is purely discriminative because it is limited to discarding those organisms that

do not overcome the requirements of the ecosystem. However, in the case of considering a sequence of *n* transitions, due to the typical variability of the offspring, the overall result can lead to the outbreak of a new species by accumulation of changes in the traits of individuals belonging to the original population (fig. 2).



The prolonged discussion between the supporters of considering the NS as a purely destructive process and the defenders of its constructive role is resolved once again by relativizing the problem. Whether the NS is assigned a creative or eliminating function depends on the way in which it is observed: in a single replacement cycle of $\langle K, I, S \rangle$ to $\langle K', I', S' \rangle$ the ecosystem screening only suppresses organisms that do not overcome it (Loewe 2008), but in a consecutive series of transitions the reproductive variability of organisms combined with subsequent ecosystem screens work out as a really modeling mechanism of differences that, by accumulation, may create types critically different from the original ones.

5. Conclusions

The popular diffusion of certain expressions converted into canons of modern science, such as the case of "natural selection", has historically expanded in parallel with the ambiguity of its interpretations (Zirkle 1941). This diffusion was fostered by the fact that the general public believed they understood what such expressions meant, and believed they understood because this expressions nested so many connotations and emotional associations that their meaning ended up being molded to the user's liking. This was the

case, for example, of the doctrine of social Darwinism, whose fatal use of the phrase "the survival of the fittest" was the perfect pseudoscientific alibi to exhibit one of the worst faces of human selfishness.

Beyond interested uses, the genuine meaning of natural selection in Darwinian evolutionism fueled secular controversies whose embers are revived from time to time shaking the never-quiet waters of epistemology. There were those who, like Popper, argued that the concept of natural selection was really meaningless, while others claimed that it meant something even if it was not clear what that meaning was.

The *KIS* scheme presented in this article aims to elucidate the basic elements of that of a wider natural scenario in which Darwinian selection is only one of the actors. Because the best way to understand the meaning is to insert it into a more comprehensive family of processes in which the general features of this term are subsumed. From such a watchtower we understand, first of all, that natural selection is undoubtedly a mechanism if by mechanism we understand a causal process that occurs in a concrete material system.

In the second place, we can also observe the multiplicity of meanings that can be assigned to natural selection, provided that we understand it as the change in only one of the elements of the *KIS* triad, the transition from one of these lists to another, or the repeated sequence of such transitions over time. Obviously, the characterization of the interactions that we have symbolized by *I* and called "ecosystem screening" will refer in general to a diverse and complex set of morphological, physiological, structural and behavioral traits with varying degrees of participation in the final survival of each individual. But despite this circumstance, the reasoning preserves its validity.

It is indeed due to the complexity of the properties and the entanglement of the interactions constituting the ecosystem screening, that the arguments are often abbreviated and the nuances of the situation are compressed by appealing to vague and excessively generic words—fitness, adaptation, adequacy, etc.— whose use in other areas, and in the absence of greater biological precision, creates in us a misleading sense of familiarity and understanding. However, just by trespassing a little the surface we discover that the alleged intelligibility is not such and, being frustrated in our expectations, it is easy to be tempted to believe that our error actually reveals the inconsistency of the concept. It is not so, certainly, and it is expected that deeper analyzes than the one proposed here will contribute to shed better light on this cornerstone of modern biology.

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