# Historicity, Temporalities, and Causality: A Confusion at the Heart of Debates on Darwinism

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**Abstract**

If Charles Darwin's work opened up the possibility of a true natural *history*, the significance of time in evolutionary processes was left unresolved. This ambiguity has led to various interpretations of what evolutionary history is, some seeing it as the pure unfolding of processes, others as a flow marked by contingency and unpredictability. These interpretations reflect underlying differences in the perception of causality: mechanical and uniform on the one hand, transformative and multifaceted on the other. This tension affects not only our understanding of the Darwinian text, but also our contemporary conception of evolutionary theory. Although many challenges in evolutionary biology are linked to time (the historicity of evolution, path-dependent processes, biological rhythms, the contingency of certain evolutionary events etc.), the importance attributed to time in biology remains unspecified. The aim of this chapter is to study the contradictions regarding the conception of history and causality in Darwin's writings and to analyse how they have permeated the different interpretations of evolutionary theory from the turn of the twentieth century to the present day. This analysis of the tensions within the different interpretations of Darwinism in history will lead me to address both the conception of biological time(s) and the approach to causality in contemporary evolutionary biology. I will conclude this chapter by proposing some clarifications about the significance of time in contemporary evolutionary biology.

**Keywords**

Time · Philosophy of biology · Charles Darwin · Evolutionary theory · Modern synthesis · French evolutionists · Process biology

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## 1 Introduction

It is often said that time, in biology, does not have the same meaning as in physics (Longo 2021). Usually, this claim aims to support the idea that evolutionary biology, contrary to most parts of physics, *cannot be* predictive because of the importance of history. Indeed, in Newtonian physics, time appears as the exploration of a space of possibilities that can be described on the basis of a limited number of propositions. This is why, even in quantum physics, where processes defy prediction, it is still possible to make probabilistic judgements about their outcomes. In contrast, biological phenomena, and especially evolutionary ones remain mostly unpredictable, and even improbable. Theorists such as Baquero (2005), Montévil (2020), and Kauffman and Roli (2023) suggest that the unpredictability of evolution stems from the fact that, in the course of evolution, it is the space of possibilities itself that changes. More fundamentally, biological entities are defined by their very history (their phylogeny), whereas physical entities are defined by fixed criteria. This conception of biological historicity is linked to the idea that causality in biology is different from physical causality. In biology, new processes emerge, whereas the laws of physics do not change. Thus, biological events can produce genuine novelties that could not have been foreseen before their emergence (Longo et al. 2012).

All these characteristics are linked to a certain conception of the role of time in biology, especially in evolutionary biology, which is rarely made explicit. The link between temporality and causality in evolution remains elusive, with the lack of historical background on this problem maintaining the vagueness. Indeed, the ambiguities surrounding the significance of historical time in biology were already harboured by Darwin's formulation of the theory of evolution and have been maintained problematically ever since. Some consider that the long time frame of the Darwinian hypothesis is uniform—allowing small variations to accumulate in a straight line. Others see it as historical time—not the simple unfolding of an unchanging causality, but a time marked by discontinuity and chance. The vagueness of the concept of biological time(s), in Darwin's writings, but also in the different formulations of Darwinian theories throughout history leads to tensions within the theory of evolution. Without clarifying the role of history, biological temporalities, and the underlying conception of causality in evolutionary theory, it seems difficult to understand the methodological and epistemological issues related to the so-called specificity of evolutionary biology in relation to other disciplines.

The aim of this chapter is twofold. The first is to retrace some debates in the history of evolutionary theory, in the light of one of its most problematic concepts: evolutionary 'time'. I want to show that some of the tensions between the different interpretations of Darwinian theory and causality in evolutionary biology highlight a lack of clarity about the historicity of evolution and the role of time in biology. The second is to provide conceptual clarifications to address issues that are generally overlooked, but which are crucial to understanding some of the epistemological challenges facing biology: How can we synthesise the different roles that time plays in our understanding of evolution? What does it mean to say that evolution is a history? Why does biological time seem different from physical time?

In order to resolve the vagueness surrounding evolutionary time(s), I begin by examining the ambiguities within the Darwinian text. I then analyse how these ambiguities have permeated the different interpretations of evolutionary theory from the turn of the twentieth century to the present day. My ambition is also to provide a clarification about what is intuitively understood when we talk about the specificity of biological time, which mainly refers to a specific conception of causality. In the last two sections, I offer some clarifications on the importance of taking different temporalities into account in evolutionary biology, and of some of the epistemological consequences.

## 2 History, Time, and Causality in *The Origin of Species* (1859)

Charles Darwin (1809–1882) did not propose any reflection on the concept of history, or on the meaning of temporality in biology. However, his theory is based on a number of presuppositions about the importance of history, the temporality of biological processes and the causality of evolution.

Indeed, Darwin's theory is based on gradualism: small individual variations, accumulated by natural selection over a very large number of generations, lead to different varieties and even different species. For the theory to explain the extraordinary diversity of biological forms, a long, even quasi-infinite time is required. But there is an ambiguity in Darwin's very theory about the conception of time.

### 2.1 A Creative History?

On the one hand, evolution is considered as a truly historical process: the flow of time is not the mere unfolding of the same processes, producing different states: it produces changes of forms. Darwin developed his theory from considerations about the age of Earth. At the time Darwin was writing, the age of the Earth was still unknown. However, Charles Lyell (1797–1875) proposed that it was at least several hundred million years old, and Darwin's theory relied on this hypothesis. "He who can read Sir Charles Lyell's grand work on the Principles of Geology [. . .] yet does not admit how incomprehensibly vast have been the past periods of time, may at once close this volume" (Darwin 1859, 282). Only the depth of geological time can explain the evolution of species from individual variations.

Indeed, for Darwin, the passage of time has an effect on biological entities: it can truly both constitute and transform species. Thus, the importance of historical time directly relates to a special conception of causality in evolution. Over the course of evolutionary history, the *same* mechanism (natural selection) produces *new* effects, incommensurable with the previous ones. New species emerge over the course of time, a novelty that is explained by the fact that the past is still effective in the present (past variations are still present in the organism). The consequence of such a theory is that new species also generate *new processes*. For example, the regulation of glucose flow by the liver is a process that only exists in species that have evolved to have a liver. The liver is an organ that has evolved historically, and its evolution has given rise to new biological processes. Thus, causality in evolution is different from causality in physics because most of the 'laws' are historically constituted (Gould 1970). In other words, the processes themselves are path-dependent (Szathmáry 2006) and naturally (though not necessarily) linked to a contingent irreversibility (Desjardin 2011).

This approach has ontological consequences: since species have evolved progressively over time, starting with small variations between individuals, they are not eternal essences, they are only *logical* categories that allow us to make differences in our classifications. Naturalists do consider that there is fecundity of mongrels and sterility of hybrids, and that species are different in kind. But, for Darwin, this is only statistical: 'it is most difficult to say where perfect fertility ends and sterility begins' (Darwin 1859, 248). There are cases where hybrids are not sterile and cases where mongrels are not fertile. Species, for Darwin, cannot be identified by fixed physico-chemical properties, since they are generated in the course of time: they are transitory forms emerging from the individual variability. Therefore, Darwin's conception of time and causality can be interpreted as relying on an ontological claim: variability is fundamental in the living (Soto et al. 2016). Indeed (1) biological entities are not specified by invariants, like in physics, but by their history; (2) the conditions of the environment are also constantly changing. This means that both observables and initial conditions always change in biology, and the combination of the two produces unpredictable processes. This would justify that, for Darwin, the *explanandum* is less evolution than the "*the preservation of favoured races in the struggle for life*" (the subtitle of the *Origin of Species*). Evolutionary time allows individual variability to be channelled and stabilised in forms that are always unpredictable. In this sense, time appears a crucial factor of evolution, enabling a very specific type of causality, different from the deterministic one present in physics.

## 2.2 Uniformitarianism

However, the evolution of species takes place *progressively*, through the operation over time of the *invariable* process of natural selection. Thus, it could be argued that the transformation of forms would happen *over the course of time* but would not necessarily imply the intervention of *new* processes generated over time (what appears as new processes would only be determined as a result of the action of natural selection). This view implies that the invariable mechanism of natural selection follows a classical causal model: it has specific effects, depending on the situation. It holds that the unpredictability of evolution does not stem from a special role of history, or from fundamental variability, but from our inability to take account of the diversity of biological situations. Evolutionary history merely unfolds invariable mechanisms.

Darwin's gradualism is indeed based on uniformitarianism, which was the key principle allowing Lyell to define the age of Earth: the causes currently at work are the same as those at work in the past. If there is a change, it must be explained by the incremental action of the processes that we currently observe operating. Thus, time is considered a uniform succession, during which changes unfold. Similarly, Darwin draws upon the brief time span of individual variations and extrapolates them into the historical time frame of species. By studying natural selection in the context of human selection, which operates on a shorter timescale, he is able to extrapolate his findings to the longer processes of nature, as if the breeders' short- and medium-term forecasting justified the uniformity of the processes (and possibly the long-term forecasting of future biological events). This view implies that each moment in biological processes is equivalent to another, and causality thus appears to be uniform. Time's efficacy does not come from a special quality, but from its quantity: the more time passes, the more transformation takes place. History, meanwhile, is reduced to a series of discrete moments, whose sum total allows for change.

Natural selection then appears as a quasi-deterministic mechanism, with little room for contingency, and time appears as a mere unfolding. This is made explicit in Darwin's early writings where he assumes that the future of species could be foreseen by a being quite close to Laplace's demon (as in Pierre-Simon de Laplace 1749–1827):

> Let us now suppose a Being with penetration sufficient to perceive differences in the outer and innermost organization quite imperceptible to man, and with forethought extending over future centuries to watch with unerring care and select for any object the offspring of an organism produced under the foregoing circumstances; I can see no conceivable reason why he could not form a new race (or several were he to separate the stock of the original organism and work on several islands) adapted to new ends. (Darwin 1909, 85)

Such a hypothesis assumes that the mechanism of natural selection leaves nothing to chance, that biological causality is as determined as physico-chemical causality, and that no new biological process can emerge in the course of natural history. So, the unpredictability of evolution is not due to any particular characteristic of living beings but to our ignorance. What seems to us to be contingency would only reveal our ignorance, the causal chain being strongly determined: "If we must marvel, let it be at our presumption in imagining for a moment that we understand the many complex contingencies, on which the existence of each species depends" (Darwin 1859, 322).

There is therefore an unresolved tension in Darwin's conception of evolutionary history and, consequently, of the causality of evolutionary processes. Darwin's theory relies on the idea of continuous variability, which can be channelled in unpredictable ways over time, generating a history in the strong sense. Emphasising this aspect of Darwinian theory, one could consider that time is not only the unfolding of invariable mechanisms but a retention of the past in the present that would contribute to the generation of true novelties. However, Darwin's conception also requires the uniformity of the laws of nature over time. Thus, in another sense, there is no real change; time appears as a mere container, with the biological processes remaining the same.

As the conception of time is ambiguous, the conception of causality remains unclear. Darwin does consider evolution to be unpredictable, as it is a "changing history" (Darwin 1859, 106), and not the mere succession of causes and effects:

> Looking to the future, we can predict that the groups of organic beings which are now large and triumphant, and which are least broken up, that is, which as yet have suffered least extinction, will for a long period continue to increase. But which groups will ultimately prevail, no man can predict; for we well know that many groups, formerly most extensively developed, have now become extinct. (Ibid., 126)

But, as mentioned above, most of the time, this unpredictability seems to reveal our ignorance of the causes at work, and not a specific sort of causality, proper to organic evolution (Ibid., 67, 79, 195 *et passim*).

Thus, the role that Darwin ascribes to time seems paradoxical: time appears to be both the mere 'container' of unchanging mechanisms and a historical time, marked by contingency and improbability, that generates unpredictable new processes.

And it is not clear that the tension can be resolved merely by relying on Darwinian texts.

## 3 Different Conceptions of Time, History, and Causality: Different Interpretations of Darwinism

The question of the specificity of biological causality and the unpredictability of evolution have consistently puzzled biologists. Some argued for more physicalist interpretations, whilst others assumed a special causality for biology. These debates, especially vivid at the turn of the twentieth century, not only relied on different conceptions of evolution but of the various temporalities, relevant to biological explanations. To demonstrate this, I will study two interpretative traditions: the French reception of Darwinism, and that proposed by some of the theorists of the Modern Synthesis.

### 3.1 Evolutionary Theory in France

#### 3.1.1 Darwinism in France

In France, the reception of Darwinism was delayed as it faced strong competition from (neo)Lamarckism. The popularity of Jean-Baptiste de Lamarck (1744–1829), especially his concept of the inheritance of acquired characteristics, may be partly due to a preference for the national author, but it also reflected a certain vision of what biology should be.[1] In France, at the end of the nineteenth century, the

[1] For a detailed overview of (neo)Lamarckism(s) in France, see Loison (2010).

biological science *par excellence* was physiology, thanks mainly to the discoveries made by Claude Bernard (1813–1878). Indeed, physiology offered the example of an experimental biological science, whose methodology was close to that of physical science, and which allowed the discovery of stable causal relationships as necessary as in physics. Physiology allowed biology to rise to the status of a 'real' science, a science based on determinism and whose hypotheses can be validated by crucial experiments. One strength of physiology is that its method is mainly experimental, relying on what can be observed *in the present*, or over a short period of time. With this in mind, it can be argued that the French preference for the inheritance of acquired characteristics inspired by Lamarckism is explained less by chauvinism than by the epistemic structure of French biology at the turn of the twentieth century. The full realisation of biology as a science depended on achieving the same level of deterministic or at least probabilistic precision as physics, which could only be attained through experimentation. Therefore, to study evolution scientifically, the mechanism underlying mutations had to be exhibited, i.e. the physiology of variation had to be understood. In this context, the Lamarckian hypothesis was particularly attractive because it suggested that the changes that cause evolution occurred during the lifetime of an individual and could therefore be directly observed and evaluated. Likewise, mutationism, supported notably by Hugo de Vries (1848–1935), was also appealing because mutations occurred within a single generation and could be studied over a short period of time, allowing for the discovery of their physiological mechanisms. Darwinism was not considered to be fully scientific precisely because the theory is based on a depth of historical time on which one could only make hypotheses but not experiments (Loison 2022). This implied that the relevant time scale for science was the short term, which makes it possible to observe efficient causality, and which we are allowed to extrapolate to longer time scales. Long, historical time, contributed nothing to explanation. Science needed to tend towards determinism and deduce a large number of effects from a small number of invariable laws—a concept that did not allow for a historical approach to biology.

This criticism of Darwinism, as untestable because based on the transformation of forms over a long period of time, was explicitly expressed by several French commentators of Darwin. The physiologist Pierre Flourens (1794–1867) was one of the first in France to provide a detailed review of *The Origin of Species*. However, he strongly opposed Darwin's ideas, and he criticised him for being unable to provide true—i.e. according to him: observable—examples of the transformation of one species into another (Flourens 1864). The same sort of objections were made by the naturalist Armand de Quatrefages (1810–1892), albeit he was less hostile to transformism than Flourens. The Darwinian theory was considered weak because it was not based on positive facts, results of experiments, which could be tested in the present (Quatrefages, 1870). One of those who welcomed Darwin positively was Charles Martins (1806–1889), director of the botanical garden in Montpellier, who republished Lamarcks's *Philosophie zoologique* (1873). In the introduction to the book, in a notable misinterpretation, he stated that Darwin consolidated Lamarck's theory. And he added that there remained, however, a great scientific task to be carried out: the physiological method needed to be applied to the study of variation if we were to understand the mechanism of evolution.

In all these authors, there was the idea that we would discover the physiological origin of species in the mechanisms of the present time, i.e. on the scale of one generation. The reference model of science remained the experimentation of the physical and chemical sciences.

Thus, there was a form of presentism (what is discovered in the present explains all past and future processes), accompanied by a nomological conception of causality. The only kind of causality envisaged was that discovered by physics—deterministic or probabilistic causality. Like the laws of physics, biological processes were conceived as immutable, history not bringing about their transformation but the successive stages of their unfolding.

### 3.1.2 French Neolamarckism: A Physiological Evolution with No History

Physiological anchoring and determinism explain both the mechanistic interpretation of Darwin in France and the success of Lamarck's theory. This coordination was especially embodied by the evolutionist Félix Le Dantec (1869–1917), a mechanist who defended the continuity of physics and biology. He subscribed to the mechanistic interpretation of Darwinism proposed by Ernst Haeckel (1834–1919), whilst at the same time calling for a new reading of Lamarck and for the physiological elucidation of the mechanisms of variation (Le Dantec 1902).

It is true that Neolamarckism is not a unified theory (for a detailed analysis, see Loison 2010). On the one hand, the first generation of Neolamarckians, including Félix Le Dantec, were fervent determinists and mechanists, who advocated for an experimental method allowing the secrets of evolution over the centuries to be elucidated in present-day experience. This was the case, for example with Edmond Perrier (1844–1921) and Alfred Giard (1846–1908) (Perrier 1879; Giard 1904). On the other hand, the second generation of Neolamarckians were vitalists and/or spiritualists who emphasised finality. This was the case with Albert Vandel (1894–1980) and Pierre-Paul Grassé (1895–1985), who considered that the theory should be complemented by a reference to the final causes, as only finality could explain the directions taken by evolution (Vandel 1949; Grassé 1973).

However, in both cases, history appears as the mere unfolding of predetermined events, according to invariable processes.

## 3.2 The Case of Henri Bergson

The philosopher Henri Bergson (1859–1941) wrote *Creative Evolution* in 1907 in this context of uncertainty about the processes at work in evolution. Although he was an evolutionist, he wondered whether the various theories of evolution under debate, be they based on mechanism (natural selection, the inheritance of acquired characteristics) or on finality (as in the vitalist interpretation of Neolamarckism) were capable of truly explaining evolution (Bergson 1911). His distrust of the debated theories stemmed from the fact that both mechanistic and finalist theories failed to comprehend the efficacy (*efficace*) of time: in one case, everything results from the initial cause; in the other, everything is directed towards the final cause. But in both cases, the passage of time between what we perceive as cause and its effect are inconsequential; any unpredictability in evolution is only due to our ignorance. In any case: "everything is given" (Ibid., 41), and history brings nothing new to the table. For Bergson, the determinism of the evolutionary theories of his time, based on a uniform and unilinear conception of causality, was linked to an inability to understand the historical dimension of biological evolution. Bergson interpreted Darwinism as such a theory, incapable of understanding the creativity of time. This led him to denounce, in both Darwinism and Neolamarckism, the inability to take into account the change of processes brought about by time. In contrast to this vision, Bergson envisaged the efficacy of time as something active. He did not think of time as a simple variable but as truly *creative*: it brings something new, the unpredictability of which comes not from our ignorance but from the very nature of history. And for evolution, in particular, Bergson proposed to think of this creative time as an *élan vital*. The *élan vital* is a propulsive and irreversible movement whose direction considered afterwards (by a retrospective glance) is like a straight line (Ibid., 124), but whose productive power has a circular dimension (living beings are like eddies, Ibid.). The objective of this image is to link, without contradiction, the directionality of time and its unpredictability. Regarding directionality, evolutionary time exhibits both linear and cyclical aspects. On the one hand, it is characterised by accumulation, an irreversible progression. On the other hand, it also involves recapitulation or resumption of the past, in such a way that history *never repeats*.

Although Bergson proposed a metaphysical conception of time that was difficult to translate into biological terms, he did clearly see that the stumbling block of the various evolutionary theories under discussion was the tension between a conception of causality based on physics and the little thought given to the importance of history.

The significance of Bergson's theoretical proposition has often been overlooked in the historiography. Biologists have been deemed uninterested in philosophical questions about the nature of historical time, which is thought to have led to a lack of serious consideration of Bergsonian philosophy in the field. If this may be generally true from the point of view of French biologists, it is not quite so simple for those who have been labelled as Modern Synthesis theorists.

## 3.3 The "Modern Synthesis"

### 3.3.1 Biogeographical Approach in Population Genetics

Julian Huxley (1887–1975) coined the phrase "The Modern Synthesis" to describe the integration of genetics and Darwinian theory by biologists from various disciplines and backgrounds (Huxley 1942). This synthesis led to a model referred to as "biogeographical" by Georges Canguilhem (1904–1995) (Canguilhem 2003, 177). Canguilhem used his term to contrast Darwin's theory with Lamarckism, according to which the environment had a physiological meaning, and what was important was the relationship between the internal and external environments. Canguilhem interpreted Darwinian theory as attributing causality to the interplay between living beings, whereby the difference between individuals structured the struggle for existence and thus natural selection. In this view, causality is based on otherness, and unfolds in *space* (and not time). Coupled with the rediscovery of Mendelian laws, this approach founded population genetics, i.e. the study of changes in allelic frequencies within a population, over time. In this perspective, time is a variable (and the difference between two varieties or two parent species is assumed to be proportional to the time elapsed). It is a measure of the difference that accentuates the effect but does not change the cause.

### 3.3.2 Creative Time and Contingency

Yet, some theorists of the so-called modern synthesis, reflected on the nature of time regarded as *historical,* i.e. as having such an efficiency that it would be *creative*. The reason is that truly new processes emerge in evolutionary history, generating an essential unpredictability. We find such reflection in Ronald Aylmer Fisher (1890–1962), Theodosius Dobzhansky (1900–1975), and Sewall Wright (1889–1988) (amongst others: Fisher 1950; Dobzhansky 1960; Dobzhansky and Boesiger 1968, 145–165; Wright 1964). And they all referred to Henri Bergson on this subject (not without criticism) as being the one who coined the link between history and creative causality in evolution—a link which, in their view, biology, unlike philosophy, cannot and should not take into account. Fisher, Dobzhansky, and Wright considered that the unpredictability of evolutionary history was related to the idea that natural selection may not be sufficient to explain all evolutionary phenomena: (1) there is a part of chance (migration, genetic drift etc. must be considered); (2) the solutions offered by evolution to ecological problems are unpredictable because biological situations never repeat themselves. Thus all three, in certain texts, questioned the nature of time as possibly producing something more than can be predicted by calculation (Dobzhansky 1960; Dobzhansky 1974; Wright 1964). According to them, in evolutionary history, the same causes cannot produce the same effects, since the same causes never occur twice.

This questioning of evolutionary temporality as truly creative comes from the recognition of the unpredictability of evolution, which is not solely attributed to our lack of understanding, but also to the historical aspect of the process itself, allowing for a degree of contingency. This contingency emanates from the fact that, in evolution, there are always original combinations of factors, combinations that have never been produced before and will never be replicated, as the factors themselves are shaped by historical processes. This prompts a more comprehensive reflection on the possibility of novelty in evolution, where novelty refers to an occurrence not predetermined in a space of possibilities.

However, it is important to note that these evolutionists questioned the creativity of evolution in papers that were more philosophical than scientific in nature. These interrogations stemmed more from the authors' personal curiosity and metaphysical reflections than from their scientific practice. To them, the question of the nature of biological temporalities, the meaning of historicity, and creativity of biological processes were not relevant to a biological theory, and should not be resolved by science but by philosophy (Wright 1964). In the background remain the idea that, for science, time cannot be anything other than a variable: a concept of creative irreversibility would necessarily be outside science. Thus, whilst all three addressed the nature of time, they did not dispute the primacy of the natural selection explanation and the biogeographical view of population genetics.

What these articles do show, however, is that the nature of evolutionary causation, and the specific concept of historical time associated with it, has not been resolved, even after the establishment of Darwinism. A tension remains, which is still evident in most contemporary debates.

## 4 A Confusion That Runs Through the twentieth Century

The problematic role of the diverse temporalities of processes played an increasingly important role in the sciences during the twentieth century. In particular, the irreversibility of time in quantum physics and the processual dimension of causal chains proposed by the theory of complex systems underlined the need for a robust concept of temporality, not confined to metaphysical debates but grounded on science theories. Hence, the (discreet) enthusiasm of certain contemporary scientists for Bergson's proposals. According to Ilya Prigogine and Isabelle Stengers, Bergson defined "a program that is beginning to be implemented by the metamorphosis science is now undergoing" (Prigogine and Stengers 1984, 83).

### 4.1 Gould, Dawkins, and Evolutionary Time(s)

However, even today, biologists rarely include a real theorisation of causality, let alone of biological time in their theories, which sometimes leads to deep misunderstandings. By way of example, it is worth mentioning a well-known disagreement, reported in detail by Kim Sterelny (2001): the one between Richard Dawkins and Stephen Jay Gould on the importance being attached to natural selection in evolution. I propose that this divergence is grounded in a more fundamental difference of perspective which, in the end, points to a dissimilar conception of biological time.

Dawkins considers time as the *framework* in which the invariable process of natural selection takes place. Indeed, in *The Blind Watchmaker,* he speaks of natural selection as an algorithm, which tends towards optimisation (Dawkins 1996, 46–50). Taking up this idea, Daniel Dennett (Dawkins' 'ally', goes so far as to conceive that natural selection might explore a 'Design Space'. He proposes that this Space contains all possible phenotypes, both in the past and in the future, and that natural selection acts as a mechanism for navigating through this space by selecting the most suitable genes to respond to ecological challenges (Dennett 1995). In so doing, Dennett reveals the implicit conception of time and causality underlying the algorithmic understanding of natural selection: time merely unfolds an invariable causality whose effects are all contained within an unlimited, yet fixed, space of possibilities.

Gould, on the other hand, adopts a historian's point of view and seeks to understand how past events can continue to have an effect today and how their significance has changed over time. First, he considers the plurality of processes at work beyond natural selection: extinction, metapopulation dynamics, and structuring of morpho-space over the centuries. Second, he focuses not only on the process but also on the specific conditions that led to the particular phenomenon under study: how variations were made available by history, and how the structuring of metapopulations in the course of history led to current biodiversity. This prompts him to (almost metaphysically) question the very nature of biological time, as a historical reality, leading to a creative causality. He grapples with the seeming contradiction that, whilst historical events are unique and unpredictable, there are nevertheless underlying natural laws that explain the recurrence of, yet not identical events. Hence, Gould conducts a reflection aiming to articulate the irreversibility and unpredictability of time—whereby the past is gone and cannot be repeated—with its cyclical nature, wherein the past retains influence and natural laws produce similar patterns of events (Gould 1988).

Stephen Jay Gould's perspective differs from Richard Dawkins' as he regards time not only as an arrow, representing a sequence of selections, but also as a cycle that allows for a resumption of events. Concretely, this means that past structures constitute reserves of potentialities that can take on new *functions* (exaptations), unpredictable from the outset—and Gould refers to Nietzsche's philosophy on this subject (Gould 2002, 1218). In the end, Gould considers the interplay between time linearity and circularity as enabling both the understanding of *contingency* (which pertains to the occurrence of unique and unpredictable biological situations) and the accounting for the fact that they have *biological and rational causes* (encompassing natural selection, morphological laws, and structural constraints) (Gould 1988).

In addition to offering an original reflection on biological time, Gould puts forward a new model of causality for thinking about the unpredictability of evolution: no longer the linear and necessary cause/effect causality, but interactions of plural, historically constituted, biological constraints producing original outcomes (Gould 2002, 1027–1037; Tahar 2022). This mixture of irreversibility and patterns leads to evolution not tending towards an optimum.

## 4.2 The Obliteration of Time

In Darwin's texts, the meaning of historical time remains a problem around which several theoretical tensions crystallize. Some examples show the creative irreversibility of time, the way in which the past extends into the present, creating 'oddities' (see, for instance, the torsion of the ovary of *Malaxis paludosa* in Darwin 2016, 200). But there is no explicit theorisation of the problems of biological temporality, and whilst it may have been considered a problem by some of the theorists of the Modern Synthesis, contemporary biology is characterised by an obliteration of time against which Gould is one of the few to speak out. As we see with Dennett's or Dawkins' theories, the temporal specificity of biological processes remains mostly unthought of, and thus neutralised. In such theories, biological history has no specificity, and the model of causality remains the same as the physical one: monolithic and nomological—ultimately uniform.

The French philosopher André Pichot denounced this obliteration of time, which leads, according to him, to evolutionary biology obliterating itself as an autonomous discipline and retreating to functional biology—whose object is not historical (Pichot 1987). Evolutionary biology is supposed to articulate phylogenetic history and the laws of functional biology, by referring both to the individual history of the organism possessing the organ or behaviour under study. But according to Pichot, this synthesis has been achieved by a cancellation of time. The phylogenetic time of palaeontology becomes the 'genetic code', or the 'genetic programme'; and individual history is reduced to being the expression of this programme. This avoids a real consideration of the effectiveness of time, by relating all historicity to a rather vague informative principle, relying on a material support. It is a way of turning the past into a piece of space in the present, of turning time into matter. The pitfall is twofold. (1) This materialisation is a cancellation (time is made space). (2) The transformation of time into space is supposed to turn its causal power into an informative one. But as the information causation in biology is not well defined, the explanations risk turning out to be purely verbal.

For Pichot, the main philosophical problem of evolutionary biology lies in this unresolved tension about the nature of time which is also an unresolved problem about the nature of causality. The historicity of evolution finds the specificity of evolutionary biology, but it is precisely this historicity that evolutionary biology refuses to consider, choosing instead to take the explanations of the non-historical sciences as a model.

## 4.3 A New Consideration of Time in Biology?

However, recent decades have witnessed a renewed interest in questions of temporality in evolutionary biology. In the philosophy of biology, more and more researchers are proposing to study life through an approach of 'process-biology', a conception in which biological causality is considered time dependent. These studies have been the subject of a recent synthesis (Nicholson and Dupré 2018), but the reflection on time remains rather classical: the authors conceive a linear time, rather close to a mere succession despite the attempt to take into account continuity (as a potential solution, some have suggested revisiting Bergson's ideas, see: Meincke 2021; Tahar 2023).

Despite its limitations, this approach nonetheless reveals a growing emphasis on the importance of time-related issues in evolutionary biology, and especially on the way in which this temporality invites us to reconsider the causality of evolution. Symbiosis, natural selection, gene transfer, posthumous phenotype. . . all these phenomena require us to study the interaction of different time scales. This is why some researchers have attempted to consider biological complexity not only causally but also temporally. This is the case of the Reticulate evolution studies which challenge the linear dimension of time and encourage us to think of complexity in a temporal way (Gontier 2016).

In these innovative approaches, time is no longer treated as a mere variable. But it is not reduced to a vague notion, which would explain the unpredictability of evolution, without it being possible to elucidate the processes underlying this unpredictability either. Instead, it is engaged in its intricate structure, moving beyond a 'merely-metaphysical label' treatment to become an operative concept for thinking about biological processes. This leads to a pluralisation of the concept of time: there is the historicity of evolution, which implies irreversibility and path dependency (in a very different sense than in physics, see Longo 2018). But there is also the problem of the entanglement of processes that take place on different timescales, particularly in the case of niche construction (Pocheville 2019). Furthermore, this approach necessitates a consideration of the diverse biological rhythms and their interplay with physical time, offering insights into their coordination (Longo 2021; see also Vaughan 2012 for a 'Bergsonian' perspective).

The subsequent sections of my chapter aim to build upon these theoretical advancements. This includes an analysis of the interrelation between the historicity of evolution and biological temporalities. Additionally, I will seek to understand the implications of these temporal problems for our comprehension of the causality of evolution and, therefore, for our ways of producing explanations.

## 5 The Creative Historicity of Evolution and the Temporal Approach to Agency

The Darwinian theory of evolution relies on the principle that variability is inherent in living organisms, both amongst individuals and across generations. Therefore, what requires an explanation is the stability or preservation of species. This means that the object of evolutionary biology is not stable: contrary to what happens in physics, the relevant observables are not invariants. Even seemingly constant biological processes, like meiosis or mitosis, are not timeless absolutes; *they are historical phenomena, having emerged at specific junctures in evolutionary history*. And nothing guarantees that these processes will last forever, even if they strongly constrain biological evolution today. Even in the historical parts of other natural sciences, history can be traced through the consistent application of mostly invariant processes over vast stretches of time (the changes are changes of values within pregiven dimensions, see Longo 2018). Biology, however, grapples with a history where processes themselves are in flux. During the course of evolution, the processes transform: they do not follow immutable types or laws but change over time. Evolutionary change is not merely a transformation of forms under fixed laws; it involves a fundamental alteration of the very 'laws' (if they can still be termed as such) governing evolution. The consequence is that time does not have the same meaning for the evolutionist as it does for the physicist: this continuous transformation of biological entities *and processes* introduces a degree of unpredictability and novelty that is unparalleled in the physical sciences.

## 5.1 The Historicity of Evolution: Beyond Uniformitarianism

### 5.1.1 Evolution: A Historical Time Marked by Rare Events

Because in the course of evolution, causal relationships themselves are transformed, each moment of time is not equivalent to another, and causality cannot be considered as uniform. Biological history is made of ruptures, contingency, and radical changes in possibility spaces. Admittedly, Darwin's uniformitarianism has made it possible to highlight the constancy of an adaptation imperative (organisms that are poorly adapted to their environment are less likely to produce offspring), which makes it possible now, as it did in the past, to explain the appearance of adaptive traits. However, this view does not account for the diversity of life forms observed and the form taken by biodiversity, nor does it predict the evolutionary paths of lineages. It may be because uniformitarianism is less an actual property of evolutionary time than a heuristic research principle, useful for understanding adaptation but potentially misleading in accounting for the diversity of biological forms.

The vast diversity in the biological world can be attributed not only to the variability of environmental conditions but also to the ever-changing biological processes through which organisms strive for existence. Because of this perpetual change, each biological event is individually *rare*, and this rarity impedes predictability (Longo 2018). This is visible, for instance, when a previously useless cryptic genetic variation begins to generate heritable phenotypic variation in a typical ecological situation. It is also the case when the environment experiences an exceptional situation (e.g. a drought that lasts only one summer), leading to the exceptional extinction of a population that was previously perfectly adapted to its environment (for a theoretical example of this, see Gould 2002, 665–666). In these cases, the event is rare in the sense that it is retrospectively improbable: it presupposes the convergence of different factors and manifests a unique complexity, itself resulting from the intersection of several histories (of the cell, the environment, the organisms, etc.). And it *disrupts* the typical sequence of causal events. The evolutionary implications of these rare events reveal that evolutionary causality is not unilinear.

In the evolutionary narrative, mathematical rarity intertwines with rarity, in the classical sense, characterised by infrequency. Certain infrequent events, though disconnected from the selective causal chains (the organisms and their environment), can exert profound evolutionary effects. A notable example is natural disasters, whose evolutionary importance has been studied and defended by David Raup (Raup 1991). Raup's hypothesis is that a certain number of species only became extinct independently of their adaptation, as a result of catastrophic events. These events would have caused cascading chains, resulting in a significant change in biodiversity, inexplicable by natural selection alone, inexplicable even by the interactions of organisms with each other and with their environment. Raup takes the example of tropical reefs: after each major extinction, species very different from those that went extinct repopulated the area. This difference comes from a time rupture. Even if the abiotic environment did not undergo much change, the rare event disrupted the evolutionary trajectories of the species that populated that environment, and these trajectories are not reproducible. This supports the idea that uniformitarianism alone is insufficient for understanding evolutionary time, as present causes may not be equivalent to those in the past. Without subscribing to Raup's radical position that catastrophes are much more central to evolution than natural selection, natural disasters do reveal that evolution cannot be predicted. And this unpredictability does not come from our ignorance but may be a property of evolutionary time itself. In the time of evolution, some events redefine the biological parameters and processes, and thus no invariants can be found. If biologists cannot produce reliable probabilistic forecasts, it is not due to the limitations of our science, but because 'the biosphere [. . .] in its persistent evolution, is doing something literally incalculable, nonalgorithmic, and outside our capacity to predict, not due to quantum uncertainty alone, nor deterministic chaos alone, but for a different, equally, or more profound reason: Emergence and persistent creativity [. . .] is real' (Kauffman 2000, x).

### 5.1.2 A Historical Causality: Constraints and Creativity

However, we do observe regularities. Meiosis and mitosis may not be eternal and invariable laws—they are indeed historically constituted processes—yet, today, they are processes that constrain future evolution. Additionally, evolution does not go in all directions: the evolutionary path of a species is linear and irreversible; convergent evolution results in similar structures in different lineages; and certain phenotypes appear inaccessible to some species (Fodor 2007). To account for these regularities, some have proposed to talk about *biological constraints* (Gould 2002; Montévil and Mossio 2015). This concept aims to replace the idea of necessitating efficient causes. In biology, there are fewer causes entailing their effects according to invariable laws than *constraints* enabling a channelling of processes at the same time as they make their transformation possible (Longo et al. 2012). These constraints are historically constituted and thus manifest the retention of the past in the present, but they are also transitory: they change under the effect of the passage of time: the future leads to their potential abolition (see Tahar 2022 for further analysis).

In evolution, processes evolve, observables change over time, and even constraints are historically constituted. Therefore, contrary to what happens in physics, history is not an exploration of a space of possibilities. Instead, historical time generates the perpetual change of the very space of possibilities, in ways that cannot be predicted (Longo et al. 2012; Kauffman, Roli 2023).

## 5.2 Evolutionary Creativity and Time-Based Approach to Agency

The creativity of the evolutionary causality comes from the following two (and correlated) properties of the evolutionary time. One is based on the Darwinian principle of individual variability but was not made explicit in Darwin's writings. (1) The irreversibility of evolutionary history results in the particularity of each biological situation: each situation is unique because an organism, like the environmental conditions in which it evolves, can never reproduce identically. The second also pervades Darwin's writing without being clearly conceptualised: (2) the irreversibility of evolutionary history has a creative dimension, made possible by the retention of the past in the present. This retention is concretely actualised in the *memory* of the living: the phylogenetic memory of genetic inheritance, but also the individual memory of the organisms, registered both in their motor mechanisms and in their cognitive ones.

This individual recording is processed differently from one organism to another: it is processed at different *rates*. This diversity in processing rates confers a distinct temporality to each organism, underpinning the originality and unpredictability of its actions. To understand this individual temporality more clearly, we can consider it in terms of three distinct but interconnected characteristics. There is the (i) *longevity of the organism*, which may be more or less out of step with the speed of change in the environment. The relationship between the longevity of individuals and the speed of environmental change plays a role in evolutionary processes. Let's imagine a population of individuals whose lifespans are short relative to the rate of environmental change. It is likely that these organisms will not have time to adapt over their lifetimes (individuals will have low adaptive capacity). However the population will evolve rapidly over the generations, with each new generation providing an opportunity for selection (the population will exhibit high evolvability). There are also (ii) *biological rhythms* (like the circadian or metabolic ones), related to longevity. These rhythms contribute to adjusting the organism to physical frequencies but are not identical to those frequencies (Longo 2021). The importance of these biological rhythms becomes especially evident when they are disrupted, as seen in cases where pollinators miss their timing with flowering plants, leading to ecological mismatches (Memmott et al. 2007). Finally, these different rhythms lead organisms to different (iii) ways of remembering the past and anticipating the future (*cognitive or psychological rhythm*). The different psychological rhythms ultimately lead to varied behaviours.

These rhythms, forming the organism's unique temporality, intertwine with physical time whilst maintaining their distinct characteristics. Their tuning with physical time carries significant ecological and evolutionary implications, influencing how organisms uniquely interact with their environments. Thus, organisms, by virtue of their temporal specificity, actively contribute to the unpredictability of evolutionary processes. In this sense, the very temporality of organisms contributes to the historicity of evolution.

Therefore, the plurality of rhythms invites us to consider the agency of organisms in terms of temporality. Darwin, without using the word agency, implicitly acknowledged it by positioning natural selection within the struggle for existence, thereby ascribing an active role to organisms in the process of selection. This perspective hinges on the idea that for a variation to be selected, it must prove useful for the organism in its interactions with the environment.

Recently, the role of organisms in evolution has received renewed attention (Corning 2014, Diogo 2017), especially through the concept of ecological agency (Walsh 2015). The main idea of this new research is that organisms *experience* the conditions of the environment as *affordances*, to which organisms respond in behaviours that both reflect the meaning the environmental conditions entail for them and potentially transform these conditions. Such an approach leads to reassess some evolutionary processes, such as the Baldwin effect (Baldwin 1896) to highlight the contribution of organisms on an evolutionary scale.

However, I suggest this conception would gain more concrete grounding if supported by a temporal approach. Indeed, a real study of the *plurality of biological rhythms* could help us understand how organisms experience environmental conditions and actualise them in unpredictable behaviours. This would pave the way for a more comprehensive approach not only to the active role played by organisms in evolution but to the link between short-term time-based organisational dynamics and long-term historical evolutionary processes.

But this understanding of evolutionary temporalities also has other implications: it reveals the specificity of biology as a historical science. Moving beyond the paradigm of the turn of the twentieth century, which predominantly viewed experimental science as the sole model for scientific inquiry, the historicity of evolution challenges us to develop new models of scientific understanding and explanation, capable of integrating the causal specificities of these temporal processes.

## 6 Nature of Time and Nature of Explanations

The implication of the above is that at least some evolutionary explanations must be historical and have a narrative dimension. This does not exclude the need for ‘processual’ explanations, i.e. explanations of how a process or mechanism (e.g. natural selection) produces a particular effect. But in evolutionary biology, these explanations need to be complemented by historical explanations whose role is not only to describe the context of an explanatory mechanism or process but to contribute to the explanation itself.

### 6.1 Historical Explanations

In evolutionary biology, several reasons require complementing the ‘traditional’ processual explanations of the nomological sciences with historical ones:

(1) Because evolution is characterised by historicity, there are no invariable laws governing efficient causes, but rather historically situated constraints. Therefore, no predictions can be made: *evolutionary explanations are mostly retrospective* and presuppose knowledge of the past (at least of phylogeny).
(2) Constraints in evolution are not monolithic but derive from a plurality of processes. Natural selection, often considered the main explanatory principle

of evolutionary phenomena, is not the sole causal process at work in evolution. Other processes, such as mutation, genetic drift, and symbiosis, also play significant roles. This requires an explanatory model capable of supporting a diversity of processes. One of the objectives of historical explanation in evolutionary biology is to *show how these various processes are articulated* to constitute constraints for the phenomenon under study.

(3) Moreover, due to the idiosyncratic nature of biological situations, these processes never generate the same effects. Thus, in evolutionary biology, there are queries that cannot be resolved by recourse to a general law, as they involve the analysis of *tokens* rather than *types* of events (Graham 1983; Tucker 2009). This is the case for inquiries such as: why does biodiversity have this configuration and not another? Or: why did this trait appear in this lineage? Or: how can we understand the speciation of this group? Hence the need for a historical explanation. Historical explanations can *account for the generation of the circumstances that enabled the occurrence of the unique phenomena under study.*

(4) In biology, each situation is a highly unique and improbable case since the space of possibilities is not predetermined but constantly changing. Therefore, *evolutionary explanations must demonstrate how a rare event occurred despite its improbability* (they should comprehend how-possible explanations, Dray 1968).

(5) Finally, because of the significance of organisms' temporal agency in evolution, *evolutionary explanations should be able to say something about the experience of organisms*, as this unique experience partially determines the evolutionary significance of the biological constraints. Without reference to this experience, part of the understanding may be lost since the rarity of evolutionary events often stems from the incongruity between the behaviour produced by organisms and the given conditions. Such an understanding of the organism's experience requires a semantic dimension that only historical explanations can support.

Therefore, historical explanations in biology are necessary, because (1) they are retrospective explanations, (2) which integrate multiple processes into a single coherent narrative. (3) They can trace the evolutionary trajectory of the case under study, (4) identify the decisive factors that made the improbable trajectory effective, and (5) formulate hypotheses about the meaning of the events and constraints for the agents who experienced them.

However, time in biology is not *only* historical. If evolution is the history of *rare* events opening unpredictable possibilities, biology is also law-based.

### 6.2 The Complementarity of Processual and Historical Explanations

The challenge is to think about how historical and processual explanations complement each other, as, at all stages of the historical explanation, nomological causality applies. According to Reydon (2021), a historical explanation accounts for the conditions that made a particular evolutionary trajectory possible (by specifying the properties of the organism, the population structure, and environmental factors), whilst a processual explanation explains how the trajectory actually occurred (specifying processes such as selection and drift). The explanatory force would thus be found in both the processual and the historical explanation.

However, given the historicity of evolution and the temporal agency of organisms, it is arguably more accurate to suggest that historical explanation goes beyond merely specifying the conditions necessary for processes to occur and may instead have explanatory precedence.

The first reason is methodological. Explaining how an event occurred in evolution requires taking into account clues from other sciences: genetics, molecular biology, but also geology, palaeontology, and so on. This necessitates the organisation of data across different systems of understanding, a task achievable only through the creation of empirically and rationally based historical narratives.

Secondly, in evolutionary biology, it is crucial to understand the articulation of the different processes in unique situations. And only a historical narrative can explain why processes interact in the way they do at a given time because the explanation must hold together different histories, characterised by different rhythms, and which are played out on different time scales. Only historical explanations can weave these stories together into coherent narratives revealing the articulation of processes.

Finally, and even more decisively, the active role of organisms in shaping their own evolutionary trajectories is not simply a contextual element that makes a process possible. And only a historical explanation can take agents into account because only a historical explanation can integrate an account of their own experience, i.e. hypothesise on the meaning biological events or constraints have for these agents, with regard to their individual history. This leads me to argue that, if the coordination of both types of explanation (processual and historical) is necessary in evolutionary biology, it is indeed history that has the explanatory priority, at least to answer some strictly evolutionary questions.

In any case, just as the historicity of evolution and the temporalities of biological processes underpin the specificity of biological phenomena, such a reflection on the complementarity of historical and processual explanations underpins the specificity of biology in relation to the other natural sciences.

## 7 Conclusion

The distinction between biological and physical time, as well as the historical nature of biological causality, are frequently acknowledged but rarely comprehensively explained. This chapter has sought to unravel the complexities surrounding the concept of time in evolutionary biology. It began with an analysis of the ambiguous conception of history in Darwin's works and the subsequent impact on the conception of causality. My aim was to shed light on how Darwin's lack of precision led to contrasting receptions of Darwinism and contradictory interpretations of causality in evolutionary biology. Moreover, I have highlighted how these uncertainties regarding the historicity of evolution, the temporality of biological processes, and their relationship to evolutionary causality have persisted from the publication of *The Origin of Species* to the present day and continue to influence contemporary epistemological issues. In the final two sections, this chapter brought together philosophical and biological perspectives to clarify these concepts and explore their methodological implications. This analysis has revealed the relationship between the temporality of biological processes and entities and the historicity of evolution, which remained implicit and confused in Darwin, and in most evolutionary biologists to this day. It has also shown the importance of revising our concept of explanation in evolutionary biology, calling for an epistemological and methodological reform inspired by the historical approach.

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