The theory of natural selection presented by Darwin and Wallace

by Timothée Flutre, PhD candidate in bioinformatics
(INRA/Paris Diderot University),
Thomas Julou, PhD candidate in evolutionary biology
(École Normale Supérieure),
Livio Riboli-Sasco, PhD candidate in theoretical biology
(Paris Descartes University)

in collaboration with Michel Morange,
professor of history and philosophy of science at the École Normale Supérieure

The texts discussed here are taken from the *Journal of Proceedings of the Linnean Society* (vol. III, 1859). The texts appear in this order:
- Letter dated 30 June 1858 from Charles Lyell and Joshua Hooker presenting the subsequent documents.
- Extract of an unpublished work on species by Charles Darwin;
- Extract of a letter from Charles Darwin to A. Gray (Boston), 5 September 1857;
- Article from February 1858 by Alfred Wallace.

INTRODUCTION

On July 1st, 1858, at a meeting of the Linnean Society of London, the groundbreaking views of two naturalists, Charles Darwin and Alfred Wallace, were presented in three texts introduced in a letter from Charles Lyell and Joshua D. Hooker, both eminent scientists of the time. This letter explains that the new theory, natural selection, concerns the production of varieties, races and species, and that it had been discovered independently by the two scientists. The emphasis, however, is subtly placed on Darwin's contribution. Why does this theory draw so much attention even now? And why is Darwin's name so well known today? While humans have always sought to understand the origin of the dazzling diversity of living creatures around them, the first systematic investigations were undertaken primarily in the 18th century. Linnaeus had given expression to the prevailing view of the time: living beings are grouped into species, which are stable, that is to say identical since their creation by God. This theory would, however, undergo successive assaults by naturalists of the day, before finally yielding to the explanatory power of the famous theory known as "natural selection". That summer's day in 1858, then, was truly a major event in the history of science in general, and of biology in particular. For the first time, a rational theory outlining a concise mechanism capable of explaining the origin and diversity of observed species was presented before an assembly of scientists.

Our objective here is to analyse Darwin's and Wallace's argument, as it was expounded in this first publication. Although these theories have gone down in history, the way they are formulated has changed over the years: for example, in the 19th century the word "evolution" was a military term describing the movement of troops changing strategic position, while the term "natural selection" would not be introduced until later on. Rereading these texts allows us to better understand the social and theoretical context that enabled such ideas to emerge. We will first present the scientific concepts, as evinced by the two authors. We will then place these reflections in the context of the scientific advances that inspired Darwin and Wallace, as well as in the social context of the scientific world of the time.

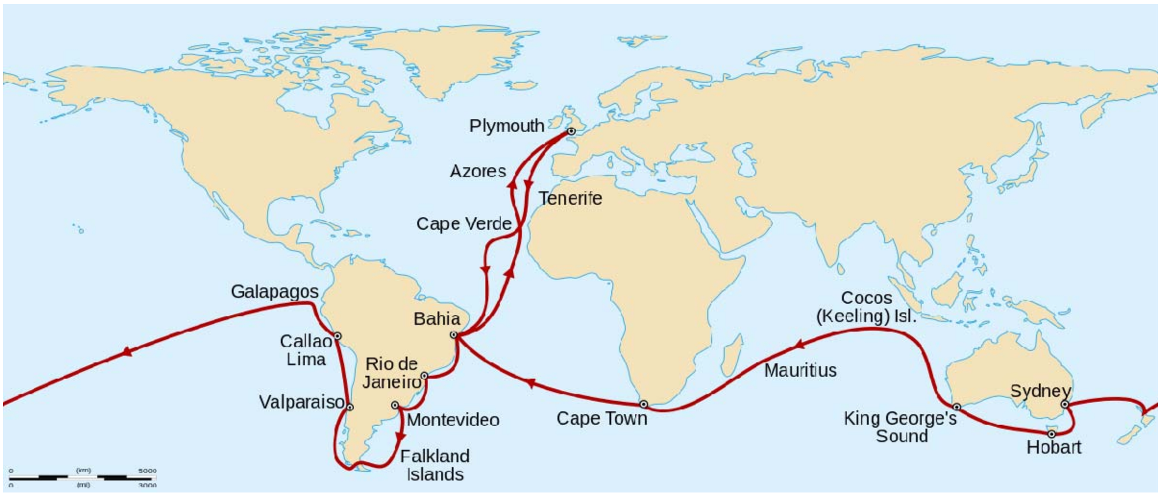

***Figure 1:* Darwin's journey on the HMS Beagle** *(December 1831–October 1836).*

Darwin, Wallace and natural selection

The major contribution of this document is the theory of natural selection. Expressed in its clearest form by Darwin, this theory holds that the evolution of species occurs through random variations from one generation to the next, i.e. hereditary variations that later give rise to selection through environmental conditions (p. 49):

> *Now, can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation in structure, habits, or instincts, adapting that individual better to the new conditions, would tell upon its vigour and health? In the struggle it would have a better chance of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better chance.*[1]

For the sake of clarity, we will present the exceptionally clear and concise argumentative structure used in the second document, occasionally supplementing it with extracts from the other two documents. We will also consider in what ways Wallace's discourse upholds the same point of view or presents divergences.

Presentation and justification of natural selection

Drawing on his observations of agronomic practices known as "selective breeding" ("when we remember what, in a few years, Bakewell effected in cattle, and Western in sheep, by this identical principle of selection"), Darwin affirms that "[s]election acts only by the accumulation of slight or greater variations, caused by external conditions, or by the mere fact that in generation the child is not absolutely similar to its parent". Darwin insists on the external nature of the factors that condition selection, the environmental conditions in nature, and the decision to select in the case of artificial selection, which in some cases also induces variations:

> *The "roguing," as nurserymen call the destroying of varieties which depart from their type, is a kind of selection.*

Though Darwin's rationale essentially rests on agronomic practices, he is bold enough to extend his conclusions to living organisms as a whole. These breeding practices strongly contributed to Darwin's understanding of the mechanisms of

1. [Translator's note] All excepts from the texts are taken from the website Darwin Online: http://darwin-online.org.uk/EditorialIntroductions/Freeman_TendencyofVarieties.html.

natural selection, and we may also assume that they determined the terminology employed. To differentiate agronomic practices from natural mechanisms, a distinction would later be made between "artificial selection" (or selective breeding)[2] and "natural selection". Darwin applies the techniques used in breeding and agriculture to wild species, advancing two decisive hypotheses: an omniscient selecting force and a very long time frame.

Darwin elevates his theoretical proposition regarding selection to the status of a "principle" and, as justification, invokes two authorities. On one hand, he argues, natural selection appears to be an extension of the vision of the struggle for life put forward by Candolle (p. 46) and Lyell and Herbert (p. 51). For these authors, this concept is related to demographic variations dependent on environmental conditions and competition between species. The impact in evolutionary terms, however, remained undetected. Selection by environmental constraints somewhat *reduces* the number of possible variations as a whole. On the other hand, the ideas of Malthus, developed in relation to human populations, are extended to other species. Darwin concludes that demography would be very different without selection, for the growth of a population, although slow, is geometric. He gives numerous examples on this subject (p. 47–49):

> *Suppose in a certain spot there are eight pairs of birds, and that only four pairs of them annually (including double hatches) rear only four young, and that these go on rearing their young at the same rate, then at the end of seven years [...] there will be 2048 birds, instead of the original sixteen.*

In terms of timescale, while it is possible to imagine the effects of breeders' practices, in a historical context it is more difficult to imagine the impact of selection on natural species. Darwin attempts therefore to facilitate understanding of this process by analogy with geological mechanisms brought to light by Lyell. The latter had suggested that vast and apparently immutable structures such as mountain ranges were in fact evolving (for example, valleys are formed by the action of glaciers and watercourses). Darwin speaks of the "almost unlimited time" and "millions of generations" over which variations accumulate and are passed on:

---

2. The term "artificial selection" refers to human intervention in the modification of the environmental conditions that influence the evolution of a species.

We have almost unlimited time; no one but a practical geologist can fully appreciate this. Think of the Glacial period, during the whole of which the same species at least of shells have existed; there must have been during this period millions on millions of generations.

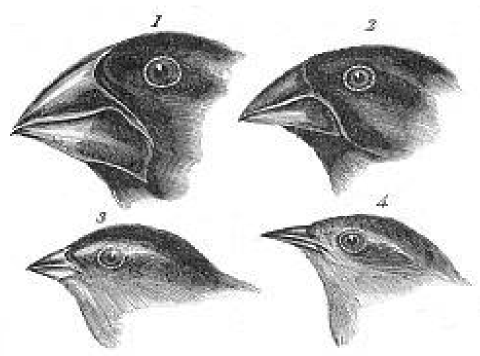

Figure 2: Darwin's finches *(Darwin, 1845:* Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. *Beagle* round the world, under the Command of Capt. Fitz Roy, *R.N., 2nd edition).*
This is the name given to a dozen different but related species identified by Charles Darwin among the fauna of the Galápagos Islands during his voyage on the HMS Beagle. *The birds are all the same size: between 10 and 20 cm. The greatest differences are found in the size and shape of their beaks. Darwin came to realise that each species inhabited a different island and that the geographic isolation had led to the development of distinct species from common ancestors. He established a direct connection between the vegetation – and thus the diet – of each species, and its morphological characteristics, notably the shape of its beak.*

Finally, Darwin summarises and recounts his vision of evolution: given the immense diversity of living forms observed, it is impossible to avoid finding variations – note the causal relationship postulated here – in particular, a few variations that confer an advantage vis-à-vis the environment (p. 52). The individuals thus formed will replace those that have retained their parents' characteristics. This is natural selection.

THE VIEWS OF A PIONEER

In both texts, Darwin presents ideas that would prove particularly clear-sighted, and which have no doubt contributed to his renown. The conclusion of the first text (p. 50), though rather precocious, already sets out the distinction between natural selection and sexual selection. Darwin contrasts the selective impact of external and environmental conditions, and the selective impact derived from choice of reproductive partners.

> *This kind of selection, however, is less rigorous than the other; it does not require the death of the less successful, but gives to them fewer descendants.*

Furthermore, in the last paragraph of the second text (p. 53), Darwin evokes a possible tree-like representation of evolution, thereby going well beyond the concept of fixist hierarchy:

> *For organic beings always seem to branch and sub-branch like the limbs of a tree from a common trunk, the flourishing and diverging twigs destroying the less vigorous – the dead and lost branches rudely representing extinct genera and families.*

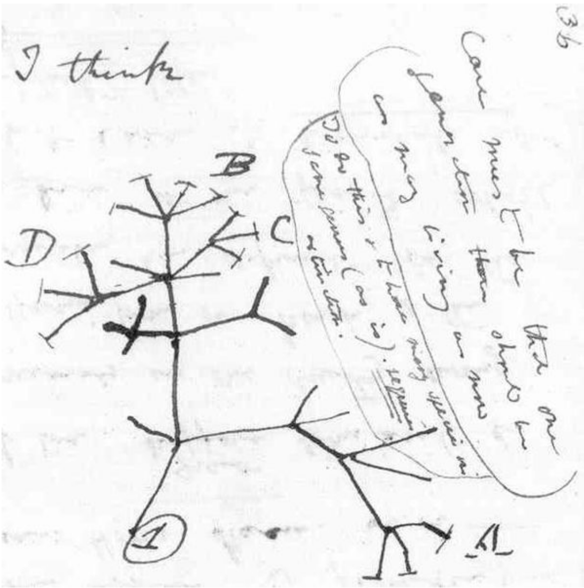

***Figure 3:* Sketch by Darwin, 1837.** *His first sketch of the tree of evolution, taken from the* First Notebook on Transmutation of Species *(1837),*
(Museum of Natural History, New York).

This arborescent classification represents the historical links between species: their phylogeny. Conceptually, it surpasses the hierarchies described by Linnaeus and integrates relationships between species, i.e. their evolutionary history, in a new classificatory approach to living organisms. This idea would be the subject of one of the rare figures in the book *The Origin of Species* but, above all, would be taken up and developed by Haeckel after 1860. It is also interesting to note that Darwin pays particular attention to the impact of the environment on the reproductive organs (p. 49):

> *It has been shown in a former part of this work, that such changes of external conditions would, from their acting on the reproductive system, probably cause the organization of those beings which were most affected to become, as under domestication, plastic.*

Did Darwin suspect that only modifications in germ cells are passed on? His suggestion that changes acquired in the somatic line cannot be transmitted to descendents would indeed be confirmed by Weismann at the close of the 19th century. Lastly, Darwin puts forward a very flexible vision of natural selection in which the rate of variation may change depending on environmental conditions (p. 49). His statement, although imprecise on this point, has the advantage of leaving scope for the recently developed concepts of “mutators” and “evolvability” (see panel):

> *such changes of external conditions would, from their acting on the reproductive system, probably cause the organization of those beings which were most affected to become, as under domestication, plastic*[3]*.*

Mutators and evolvability

These modern concepts explain what are known as second-order evolutionary mechanisms. In certain conditions, under the influence of so-called “mutator” alleles, the genetic mutation rate of an organism can increase or decrease. These mutator alleles correspond to alterations in the copy or repair systems of DNA, whose accuracy diminishes. Hence numerous errors will remain in the replicated genetic material.

This mechanism, discovered in bacteria, has revolutionised our view of the relationship of living organisms to evolution. For example, it should be considered that in conditions of environmental stress, the variability of

[3] Darwin’s use of this term suggests he did not consider plasticity as necessarily constant.

individuals within a given species – which is acted upon by natural selection – may itself vary. The scale of these mechanisms is described in terms of "evolvability".

While Wallace's reflections on these issues certainly do not display the same range, we should note his surprisingly modern analogy between natural selection and the regulatory system of the steam engine (p. 62):

> *The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident.*

Furthermore, Wallace introduces a concept that is absent in Darwin, and which would be taken up regularly by others, that is the tendency of species to become more complex as a result of natural selection. This issue is still subject to debate.

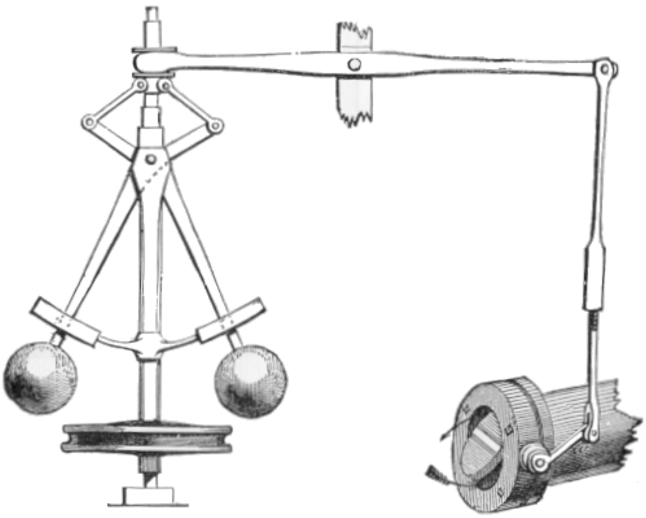

***Figure 4:* The centrifugal governor (1788) of Watt's steam engine.**
It is a retroactive mechanism: the faster the motor shaft on the left rotates, the further the balls move apart, thereby causing the steam valve on the right to shut, which regulates the speed of the motor shaft.

DIFFICULTIES IN THE TEXT

While of course recognising the excellence of the conceptual advances found in Darwin's and Wallace's argument, it is important to identify a number of weaknesses in the text, notably aspects that would later be modified by the authors themselves or by future generations of evolutionists.

Darwin bases his entire argument on his observations of what would be termed “artificial selection”, positing that changes of similar importance must be induced by natural selection. However, he does not extend the analogy to the point of imagining that rates of evolution may be comparable, in which case important changes could be observed by humans in species that reproduce rapidly, such as microorganisms. On the contrary, he repeatedly insists on the great length of time necessary, implicitly exploiting Lyell’s credibility. This might be seen as inconsistent with his reasoning, considering that the two processes are of a different nature. In addition, despite the attention Darwin pays to demography, he is reluctant to consider the idea that it may be possible to pinpoint individuals eliminated by natural selection (“[…] we ought to feel no surprise at our being unable to discover where the check falls in any animal or plant”). This point of view – combined with the former – makes his views impossible to test, as the processes take too long and are without visible demographic effect. And yet, a few decades later Dallinger would demonstrate the selection underway among unicellular algae, in an experiment that would last seven years, from 1880 to 1887.

Heredity, however, is the weakest aspect of the theory of natural selection as Darwin and Wallace present it here. Neither of the two authors possesses a theory of heredity and they therefore discuss this selection – which riddles organisms by favouring those who inherit advantageous characteristics from their parents – without knowledge of how such characteristics are passed from one generation to the next. In the same period, the Czech Gregor Mendel (1822–1884) had put forward an explanation, but Darwin was unaware of his work. It was not until the 20th century that the advent of genetics would propose sound explanations for the hereditary mechanisms in play, thereby enabling these points of views to be unified within a comprehensive conceptual framework.

From Darwin’s vision emerged the idea that species can attain an evolutionary optimum within a given environment. Nevertheless, Darwin considers that a species adapted to a given context can lose its “optimal” position if the environment is altered. “High-quality” species therefore exist only in a given context. Similarly, modern formulations of natural selection consider local optimisations from an environmental as well as temporal point of view. Thus, since Darwin's day comparative and experimental studies have shown that selection is not directed and could lead to solutions that are not necessarily advantageous in the long term.

Likewise, Darwin mentions that "small" and "large" changes can take place, but he does not clearly explain whether they can have different roles. In addition, nothing is said as to the rate at which these changes arise: are the small ones more frequent than the large? Such questions are still the subject of ongoing research.

A THEORY EMBEDDED IN AN HISTORICAL CONTEXT

Darwin's and Wallace's thought was not forged in isolation but rather in a very prolix scientific context. At the time, a great number of theoretical propositions attempted to explain, more or less cogently, the diversity of living creatures and, occasionally, their evolution. In some ways, Darwin succeeded in combining numerous ideas that had been formulated separately by different scientists. More generally, it is nowadays considered that great scientific innovations emerge from a combination of a small number of pre-existing but separate ideas emanating from distinct disciplinary fields. Thus, to better understand the conceptual advances expressed in this document, it is important to understand the breadth of the ideas on which Darwin and Wallace were able to draw.

ON FIXITY, OR THE EVOLUTION OF SPECIES

The theory of natural selection is, in its essence, an evolutionist theory. But many other theories had come before it, each of which aimed to explain the diversity of natural species.

Fixism holds that each living creature belongs to a single species alone, and that species are fixed: there is no transformation and therefore no speciation. Species do not evolve – and have not since they were created. As a consequence, there exists a classification of the living world as it was conceived, and updating it would enhance our knowledge of living organisms. Within this theory, the taxonomy of the Swede Linnaeus (1707–1778) is authoritative. In his *Systema naturae*, first published in 1735, Linnaeus established a hierarchy (classes, orders, genera, species, varieties) as well as a binomial nomenclature, both of which are still in use today. Linnaeus believed that *Nomina si nescis, perit et cognitio rerum* ("If you know not the names of things, the knowledge of things themselves perishes"). The French botanist Jussieu (1748–1836) would pursue this work and improve on the Linnean classification. To do so, he used a larger number of characters.

Confronted with problematic observations such as agricultural varieties of plants that differ from species found in nature, fixism responds by imagining them as accidental but reversible changes, capable, depending on the environment, of reverting to the species as it was initially conceived. However, fixist arguments were sometimes more artificial, ad hoc or even deistic than they were rational. For example, in his *Genera plantarum* of 1737, Linnaeus decreed that "[t]here are as many species as the infinite being created diverse forms in the beginning". Furthermore, Linnaeus's classificatory work led him to divide the human species into different "races". He was opposed for these ideas by French philosophers and naturalists including Diderot, Buffon and Maupertuis.

Some scientists felt the need to amend the fixist theory, but did not dare topple it further. In his studies of comparative anatomy, Cuvier (1769–1832) observed that fossils in deeper strata differed more from current species than those in recent strata. He also remarked that some types of organisms are no longer in evidence in the higher strata. He therefore posited several episodes of creation interspersed with catastrophes in which some species disappeared. Within each episode, however, he maintained a fixist framework of thought.

Other thinkers, notably Maupertuis (1698–1759), who was interested in the concept of heredity, had no qualms about attacking fixism, suggesting that species evolve throughout time. His ideas – remarkable for his time – make him a distant precursor to genetics: a series of fortuitous and repeated mutations can engender new species. He set out his intuitions in *Vénus physique* in 1745:

> *It is thus that in a deep mine, when the seam of white marble has run out, one finds only stones of different colours succeeding one another. It is thus that new races of men may appear on Earth, & the old ones may pass away.*

Buffon (1707–1788), for his part, put forward a theory of degeneration. Some species are derived from the degradation of initial "high-quality" species, as the donkey from the horse. The degenerate species can, however, revert to the initial species when placed in adequate conditions.

It is with Lamarck (1744–1829) that the idea of the evolution of species takes shape. His many works would contribute much to the biological sciences. Besides coining the word "biology", he proposed a theory of evolution based on two principles: the tendency towards greater complexity and the influence of surroundings. Species evolve through the transmission of modifications acquired throughout the course of life; this is the inheritance of acquired characteristics (*Recherches sur l'organisation des corps vivants* ("Research into the Organisation of Living Bodies"), 1802):

> *Each change acquired in an organ by a habit of use sufficient to have caused it is then conserved by generation, if it is common to the individuals that in fecundation cooperate together in the reproduction of their species. Finally this change propagates itself and thus passes to all the individuals that follow one another and that are submitted to the same circumstances, without them having been obliged to acquire it by the way that really created it.*[4]

In this path he would be followed notably by Geoffroy Saint-Hilaire (1772–1844), who would confront Cuvier in epic discussions before the Académie des Sciences.

Across the Channel scientists were also pondering these questions. In 1795 the Scottish geologist James Hutton (1726–1797) suggested that the Earth had been formed gradually, in successive layers. According to gradualism, every profound change is the result of the accumulation of slow processes, in slow stages; this conception is therefore opposed to catastrophism. Charles Lyell (1797–1875) would incorporate this idea into his theory of uniformitarianism, according to which the geological processes at work in the distant past are still underway.

THE STRUGGLE FOR LIFE

4. [Translator's note] Cited in Richard J. Burkhardt Jr, "Lamarck, Evolution, and the Inheritance of Acquired Characteristics", *Genetics* 194(4), 2013, DOI: 10.1534/genetics.113.151852, http://www.genetics.org/content/194/4/793.full.

Another argument essential to the theory of natural selection is the ruthless struggle for life observed by many naturalists, and far removed from the harmonious vision presented by some. The botanist Augustin de Candolle (1778–1841) worked with Lamarck on *Flore française*.

Figure 5: The Swiss botanist Augustin Pyrame de Candolle (1778–1841).
He is cited several times by Darwin.

He notably studied the effects of the physical environment (soil, temperature, sun, water, altitude) on the geographical distribution of plants as well as the role of interspecies competition for resources (*Essai élémentaire de géographie botanique*, 1820):

> *[...] let us consider in this regard the plants of a single land that provides a great variety of localities; all these plants are in a continual state of war; the first to establish themselves in a place exclude the others, the large stifle the small, the perennials stifle those with shorter life spans, the most fecund drive out those who multiply with more difficulty [...].*

Nevertheless, he remains fixist:

> *It is plain to see that all these discussions about the laws of distribution of plant life in the world rest essentially on the opinion of the permanence of species, an opinion supported by numerous arguments and which one can attack only be neglecting well-known facts and consigning oneself to ill-known facts.*

In the same vein, and influenced by poor harvests in 1794 and 1800 in England, the economist Malthus (1766–1834) rose to fame through his work on the relationship between population growth and the growth of output. He expounded his views in his book *An Essay on the Principle of Population*, published anonymously in 1798 and of which the sixth and final edition, published in 1826, would influence Darwin and Wallace. He notably writes:

> *Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. […] By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal. This implies a strong and constantly operating check on population from the difficulty of subsistence.*

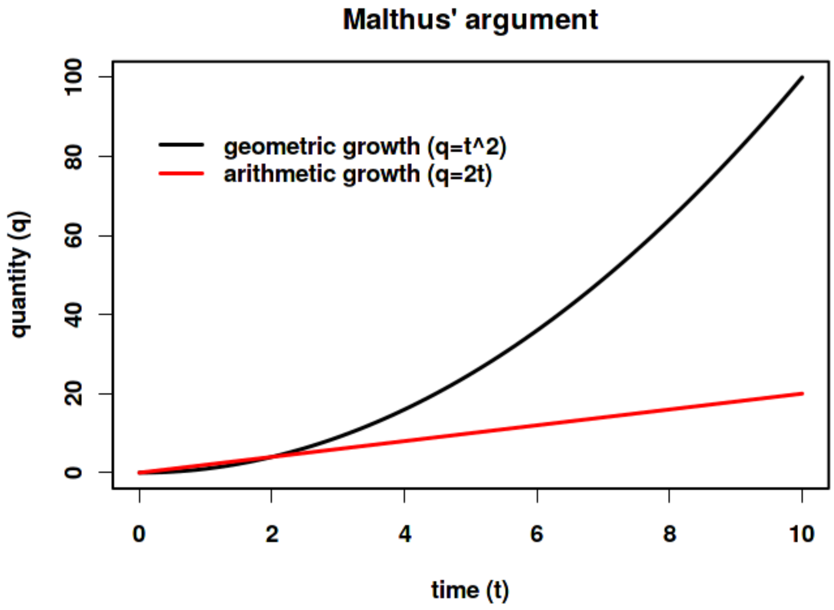

Figure 6: Malthus's argument. *Arithmetic growth (red line), according to Malthus, describes growth in the means of subsistence, while geometric growth (black curve) describes population growth.*

THE COALESCENCE OF A SYSTEM OF THOUGHT

Darwin's ideas, set out in the first paragraph of this paper, were naturally enriched by the concepts presented above and the observations on which they hinge. For example, it is evident that Darwin imports Candolle's ideas about the struggle between individuals for survival and supplements them with the evolutionist ideas of Maupertuis and Buffon, before, like Malthus, drawing together the various strands. When he adds to this his observation on practices known as “selective breeding”, one can easily see in hindsight that he had successfully expounded the principle of natural selection.

Darwin was also able to gather together *in situ* observations, interpretations of fossils, mathematical concepts, theories about animals and others about plants – all of which emanated from thinkers working in different contexts or even writing in different languages. This synthesis of so many diffuse observations and ideas into a concise and limpid theory should be credited to Darwin’s indefatigable capacity for reflection and abstraction.

DIFFERENT SCIENTIFIC POSTURES

Rooting one’s work in a scholarly context does not, however, exempt a scientist from engaging in the society of other scientists of the day. Today, a researcher would be hard pressed to move forward without dedicating a considerable amount of time to discussion with his or her peers and evaluation of others’ work. Science is a world with its own rules and values. It is therefore essential to show gratitude to scientists, without whom we could not undertake further research. It also useful to be able to criticise the work of others on the basis of sound arguments and while remaining courteous. The academic world can sometimes be cruel to those who deviate from social norms, regardless of the scientific value of their ideas.

The impact – and acceptance – of the propositions put forward by a scientist depends in large part on their place within the scientific community, and the manner in which they express themselves, again regardless of the period or discipline. Above and beyond the issue of scientific argument, Darwin and Wallace differed in important respects in terms of their scientific demeanour, which may have had a significant impact on the perception of their theories.

SOCIAL POSITION WITHIN THE SCIENTIFIC COMMUNITY

Thanks to his text, Darwin takes up his place in a line of great scientists. He does not refer directly to the conclusions of their work but metaphorically imports the conceptual dimensions produced in the work of his peers. In biology, for example, he injects a new temporal dimension, one formulated by Lyell and explaining that observed landscapes are the result of the action of water and wind over millions of years.

The field of disciplines invoked by Darwin is much broader than in Wallace's text (geology, epidemiology, biology, agronomy, etc.). Darwin thus positions himself in a theoretical frame that draws is force from principles beyond the simple observation of the biological field, and he integrates these principles into a new way of thinking about natural systems.

Wallace attacks Lamarck directly and undiplomatically, which Darwin does not venture to do:

> [Wallace] *The hypothesis of Lamarck – that progressive changes in species have been produced by the attempts of animals to increase the development of their own organs, and thus modify their structure and habits – has been repeatedly and easily refuted by all writers on the subject of varieties and species*.

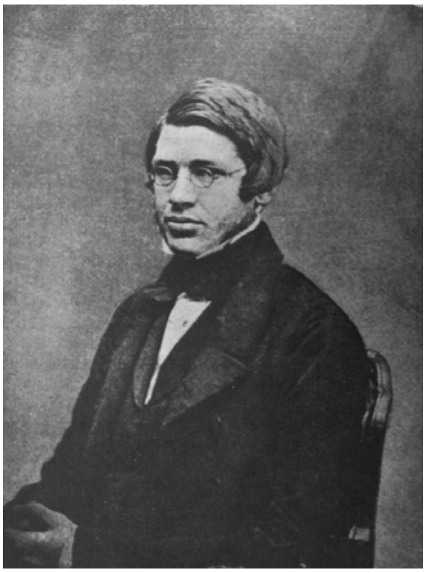

***Figure 7:* Alfred Russell Wallace (1823–1913)**

Wallace, clearly confident about his propositions, nevertheless feels the need to oppose other conceptions. Darwin, for his part, does not seek to contest anything at all. The style of his discourse leaves the impression that the concepts he puts forward are self-evident, which some might interpret as a kind of pretension – but one which to some extent would be justified by history.

***Figure 8:* The Darwin-Wallace Medal, 1908 (head & tail).** *It was issued by the Linnean Society fifty years after the presentation of their work in 1858 (the texts of the Linnean Society commented on here).*

CONTRASTING STYLES

The two authors can also be contrasted in terms of their writing style, which there again reflects their scientific demeanour. Darwin is concise, even elliptic; the logical sequences are accentuated by clear numbering (this numbering of arguments would also be used in *The Origin of Species*, 1859). The text flows extremely well. One senses the author's thorough mastery of the subject. One also senses that he could say much more, that the theoretical consequences of the issues covered extend far beyond the domains in which Darwin has forged his theory. While Wallace confines himself to a rigorous analysis based essentially on observations of varieties used in breeding, Darwin puts forward observations of different animals as well as plants.

In addition, it is important to note that Darwin uses metaphors, allowing us to imagine more than what is said in the text. He also has recourse to mathematical models (model of geometric growth) and gives numerical examples ("2048 birds", p. 47), a practice then rare in the life sciences.

It is also worth asking whether it would be possible, in today's scientific literature, to find a text of similar scope to Darwin's. No scientific author could set out such a radically new theory so elliptically and admit to having discussed it with many individuals, while having published nothing for years. We would ask that such a theory be based on more rigorous experimental observations or at least that the author provide predictions of the results of future experiments that would corroborate – or not – the theoretical propositions. We could, however, find such kinds of theoretical propositions in books, but supported by many citations referring to experimental work.

WHY IS DARWIN REMEMBERED BY POSTERITY?

Reading these three texts, one can rather reliably conclude that history has essentially vindicated Darwin's propositions. To vindicate Darwin is to vindicate the force of a theoretical system of thought that paid little heed to the constraints of embryonic scientific formalism. It also vindicates a scientific system of thought that ventures beyond the domains in which it was forged. Though Darwin was a naturalist, he understood geology and demography and strove to achieve coherence between the theoretical bases of these disciplines. He did not see why such disciplines should function in radically different ways.

CONCLUSION

In the 20th century, biology witnessed the unification of several sub-disciplines to form modern evolutionary synthesis, in order to explain as comprehensively as possible the evolution of living organisms. Natural selection occupies an important place here, as is confirmed notably by work in population genetics and ecology. The premises of the current conception of evolution, expounded in the 19th century, are still therefore relevant.

And yet, though he proposed a sound theory for the origin and diversity of species, Darwin left his successors an immense task and posed countless new questions. How can the effects of selection be measured, namely how do they change over time as well as in relation to population size? What are the links between the impact of variations (mutations) and their occurrence ratio? How does selection operate at each level of the organisation of a “complex” system?

The 21st century, with its array of technological innovations, will no doubt enable scientists to advance our understanding of these phenomena a little further, following the path opened up around Darwin.

■

(December 2009)

(Translated in English by Helen Tomlinson, published September 2014)