

Wallace's and Darwin's natural selection theories

Santiago Ginnobili^{1,2} • Daniel Blanco^{3,4}

Received: 28 December 2016 / Accepted: 5 July 2017 © Springer Science+Business Media B.V. 2017

Abstract This work takes a stand on whether Wallace should be regarded as coauthor of the theory of natural selection alongside Darwin as he is usually considered on behalf of his alleged essential contribution to the conception of the theory. It does so from a perspective unexplored thus far: we will argue for Darwin's priority based on a rational reconstruction of the theory of natural selection (following a hierarchical perspective for scientific theories, we present its conceptual framework together with its fundamental and special laws) as it appears in the writings of both authors. We show that the theory does not appear in exactly the same manner in the writings of each of its alleged co-discoverers: tough we find the same fundamental elements in both works, even in Darwin's early texts, we discern a more complex unifying and ramified structure than the one we find in Wallace's Ternate manuscript. Even when we think the badge of the "Darwin–Wallace" theory is well deserved, the unifying

Equal time was dedicated to the production of this article. Order of authorship was decided by chance.

Santiago Ginnobili santi75@gmail.com https://santi75.wordpress.com

> Daniel Blanco danielblanco.fb@gmail.com

- ¹ National Council of Scientific and Technical Research (CONICET)/Center for Philosophy and History of Science (CEFHIC)-National University of Quilmes (UNQ)/University of Buenos Aires (UBA), Buenos Aires, Argentina
- ² Instituto de Estudios sobre la Ciencia y la Tecnología, Roque Sáenz Peña 352, B1876BXD Bernal, Provincia de Buenos Aires, Argentina
- ³ National University of the Littoral (UNL), Santa Fe, Provincia de Santa Fe, Argentina
- ⁴ IHuCso "Litoral" UNL-CONICET, Sede-Facultad de Humanidades y Ciencias-FHUC, Ciudad Universitaria, Paraje El Pozo. (3000), Santa Fe, Provincia de Santa Fe, Argentina

force of Darwin's version has proved to be one of the keys for the ulterior success of the so-called Darwinian revolution in Biology.

Keywords Darwin \cdot Hierarchical view of theories \cdot Natural selection \cdot Theory of natural selection \cdot Unifying power \cdot Wallace

1 Introduction

Alfred R. Wallace (1823–1913) is typically regarded as co-originator of the theory of natural selection alongside Charles R. Darwin (1809–1882), having made an allegedly essential contribution to the conception of the theory.

There is an extensive literature by well-informed writers on the issue of the coauthorship of the theory of natural selection, and we include many of their works in the bibliography. This paper adds to this list, but it does so from a perspective unexplored thus far: we will argue for Darwin's priority based on a rational reconstruction of the theory of natural selection as it appears in the writings of both authors. In doing so, we will try to show the relevance a philosophical approach to the theory of natural selection has for the historiographical issue of priority. We will show that even though we regard the extreme stances to be excessive, the theory of natural selection does not appear in exactly the same manner in the writings of each of its alleged co-discoverers.

Many authors estimate that the Darwinian theory of natural selection cannot be found in Wallace's texts at all, placing Darwin as its only discoverer. We make a case for Darwin's priority following a stronger strategy. Even if we conceded to those who argue for the co-authorship thesis that there exists a relevant sense in which both theories (the one proposed by Darwin and the one proposed by Wallace) share the same (or very similar) fundamental concepts, and that these concepts are related to each other in the same (or a very similar) way, at the most, what can be maintained is that Wallace glimpsed only a small (though important) part of the Darwinian selection theory. In this case, and as we will show, Wallace's theory would be a specialization (in a technical sense that will be detailed later) of Darwin's theory. (Note that a conclusion based on a systematic approach can be made independently of chronological issues.) Furthermore, if we admit that the explanatory success of the theory of natural selection resides in its unifying power (as is the case with most broad scientific theories), and if such unifying power can only be found in the Darwinian version of the theory, then virtually all the conquests selectionism has achieved are due to Darwin, not to Wallace.

Our analysis will focus mainly on Wallace's Ternate paper and Darwin's *On the Origin of Species* (henceforth *OS*), but it will refer to texts written by Darwin prior to 1858 that are central because they were developed in the absence of any influence from Wallace, whereas *OS* was, arguably, not.

The paper is organized as follows:

In Sect. 2, we introduce the historical facts regarding the so-called co-discovery. These facts will underlie our meta-theoretical discussion.

In Sect. 3, we reconstruct the theory of natural selection succinctly and intuitively, presenting its conceptual framework, together with its fundamental and special laws.

We base this reconstruction on the mature formulation of the theory as it appears in *OS*. Beforehand, we briefly present the meta-theoretical perspective that we employ.

Clearly, the correctness of our conclusions depends on the adequacy of this reconstruction.

In Sect. 4, we will examine whether this theoretical structure can already be found in Darwin's texts prior to 1858, especially in the draft he wrote in 1842, and in his far longer and more sophisticated essay of May 1844.

In Sect. 5, we will present the theory as found in Wallace's 1858 paper, so that it can be compared with Darwin's. There, we will be able to determine whether there are enough coincidences between the two for us to hold that they had—after all—arrived at "exactly the same theory".

Finally, in Sect. 6, we argue for our position on this controversy and make explicit the sense (if there is any) in which the epithet of "co-discoverer" may be deservedly ascribed to Wallace.

2 The not so-uncontroversial facts

Briefly, the facts that are usually taken as uncontroversial are these: Wallace, under the influence of Vestiges (McKinney 1966, 1969; Secord 2000, pp. 332-333), first suggested the key insight that species morphology transforms through time, or "transformism", in the decade of 1840, and clearly states the thesis in the "Sarawak manuscript" of February 1855 (Wallace 1855; cf. Kutschera and Hossfeld 2013; van Wyhe 2016), whereas the oldest records of Darwin's evolutionary insight date between 1835 (shortly after the HMS Beagle left the Galapagos Islands) and the beginnings of 1837 (after his return to England), following an interview with the prestigious ornithologist John Gould (see Sulloway 1982, 2009; cf. Hodge 1983a, b, 1985, 2010; Hodge and Kohn 1985). On the other hand, the first published work describing the theory of natural selection is Wallace's "Ternate manuscript" (cf. Kutschera and Hossfeld 2013; Smith 2015), dated February 1858 (Wallace 1858);¹ whereas Darwin sketches the theory (in limited form) by the end of 1838. In the case of Darwin, the development of the theory is recorded in his informal annotations and in two essays at the beginning of the decade of 1840 (Darwin 1909a, b), and afterwards, from 1856 onwards, in an extensive book, Natural Selection, an unfinished text that appeared in print only in 1975 (Stauffer 1975; cf. Hodge 1977), and of which OS is but a summary. Once the Ternate manuscript came to Down House, and after some hesitation, Darwin edited down his long work into an abridged version that became OS.

Additionally, although many contrasts between the two can be drawn, several authors have voiced the numerous coincidences concerning the context of discovery of the theory, such as the following (with no intention of being exhaustive):

- both became naturalists of transoceanic expeditions (Burstyn 1975; Darwin 1839; Gruber 1974; Wallace 1853, 1869b);
- both wrote down notes with their speculations on the "mystery of mysteries" on little easy-to-carry notebooks (Barrett et al. 1987; Hodge 1985; Hodge and Kohn 1985; Costa 2013);

¹ Remarkably, Wallace did not use the expression "natural selection". See note 14 on his opinion regarding the use of this nomenclature.

- both mention insular and continental biogeography as a trigger for their ideas (Bueno Hernández and Llorente Bousquets 2003; Camerini 1993; Darwin 1859, Chapters 11–12; Michaux 1966; Wallace 1870, 1880, 1889, Chapter 13; Wallace 1891);
- both read in works of Edward Blyth (1810–1873) notions that anticipated rudiments of their own ideas (Beddall 1968, 1972, 1973; Blyth 1835; Costa 2013; Darwin 1861, p. 19; Eiseley 1979; Gould 1987, pp. 51–61; Krimbas and Krimbas 2004; Schwartz 1974);
- both confessed to having been heavily influenced and inspired by Charles Lyell's (1797–1875) *Principles of Geology* (Lyell 1830), a work both read while in their respective journeys out of England (Costa 2013; Darwin 1958, pp. 77, 101–102, 119; Fichman 2004; Hodge 1985; McKinney 1972; Recker 1990; Wallace 1870, pp. 13–14, 1905, p. 355);
- both link the reading of *An Essay on the Principle of Population* by Thomas Malthus (1766–1834) (Malthus 1798) with the discovery of natural selection (Darwin 1861, p. 4, 1958, p. 120; Hodge and Kohn 1985; Moore 1997; Slotten 2004; Wallace 1858, 1905, pp. 232, 240, 361; 1909, pp. 130–191); and,
- both went through a relatively brief period between the statement of the *explananda*—transformism, the determination of adaptations, etc.—and the formulation of the *explanans*, the theory of natural selection: as mentioned, 1855–1858 for Wallace; 1837–1838 for Darwin (Hodge and Kohn 1985; cf. van Wyhe 2016).

Regarding the alleged co-authorship of the theory, the vast majority of historical expositions place Darwin and Wallace on a par, with the significant caveat that there is an enormous amount of textual evidence showing that Darwin started thinking about (and collecting data for) transformism and natural selection long before his colleague (the aforementioned maturing process going from 1838 to 1858/9).

Nevertheless, there are cases that prevent this consensus from being unanimous. To consider only the most extreme stances, let us indicate that, on the one hand, Eiseley (1958, 1979), Brackman (1980), McKinney (1966, 1972), Lloyd et al. 2010, and Brooks (1969, 1972), among others, hold that it is Wallace who deserves the main credit instead of Darwin. According to this version of history—that in the case of the first two authors has conspiratorial implications—Darwin is more indebted to Wallace than is acknowledged in the "official story" (cf. Beddall 1988). On the other hand, Bock (2009) and Caponi (2009) hold, for different reasons, that it is exaggerated to read Wallace's 1858 piece as including the theory of natural selection or the Principle of Divergence (cf. Brooks 1969, 1972), and that his contribution has simply been overestimated by history. Other authors introduce nuances of these positions (cf. Kutschera and Niklas 2004, pp. 256–257; Levit and Hossfeld 2011, p. 302; Costa 2014, Chapter 5).

Of course, we cannot overlook what our two candidates themselves have said on this delicate matter. Wallace, on the one hand, viewed himself as second when it came to claiming any credit and displayed no shame or jealousy about it. He called himself "a Darwinian"; in his mature age he gave the title "*Darwinism*" to one of his most widely read evolutionist works (Wallace 1889); towards 1898, he places "the name of Darwin on a level with that of Newton" (Wallace 1898, p. 143); and in 1908 he openly defended Darwin's priority.² Darwin, on the other hand, both in private correspondence³ and in public writings, gave Wallace the role of co-discoverer of "exactly the same theory" (Darwin 1958, p. 121).

In addition, although most authors state the co-authorship whenever the question is explicitly raised, it is undeniable that, ignoring a few exceptions, and especially since Darwin's demise, history of science neglected Wallace for the most part. Even though his participation in the genesis of the theory of natural selection is mentioned in most cases, the space devoted to his work is too often reduced to a few marginal commentaries in each exposition (Beddall 1968; Brooke 1984; Costa 2014; Hossfeld and Olsson 2013; Kutschera 2003, 2008; Lloyd et al. 2010; McKinney 1966, 1972). (Note that the usual terminology for the transformist theory and/or the natural selection is "Darwin's theory", whereas "Darwin's and Wallace's theory" is far less frequent, and even less so is "Wallace's and Darwin's theory".) This tradition of placing Wallace second can be observed even today in the vast bibliographic production of the so-called "Darwin industry" (greatly increased in 2008/9 for obvious reasons), which contrasts with the few and valuable works dedicated to Wallace (a contrast somewhat weakened in 2013 for, again, obvious reasons).

3 The structure of the theory of natural selection

3.1 Sketch of the meta-theoretical perspective employed

To achieve our goals, we make use of rudiments of the hierarchical perspective on scientific theories, which are tools that are common to various representatives of the so

² In Wallace's own words (Wallace 1908, pp. 5–7):

Since the death of Darwin in 1882, I have found myself in the somewhat unusual position of receiving credit and praise from popular writers under a complete misapprehension of what my share in Darwin's work really amounted to. It has been stated (not unfrequently) in the daily and weekly press, that Darwin and myself discovered "natural selection" simultaneously, while a more daring few have declared that I was the first to discover it, and that I gave way to Darwin! [...] He [Darwin] would have been at once recognised, and should be ever recognised, as the sole and undisputed discoverer and patient investigator of the great law of "Natural Selection" in all its far-reaching consequences.

³ Despite subsequent debates [see the well documented work of Malcolm Kottler on this (Kottler 1985)], both Darwin and Wallace stressed the similarities when discussing originality. In 1858, and after receiving Wallace's Ternate paper, Darwin wrote two famous letters to his close friend Charles Lyell, expressing desperate worries regarding priority. In the first one (dated June 18th) he wrote: "I never saw a more striking coincidence [between his ideas and Wallace's]. If Wallace had my M.S. sketch written out in 1842 he could not have made a better short abstract! Even his terms now stand as Heads of my Chapters." (Burkhardt and Smith 1992, p. 107) In the second letter (dated June 25th) he wrote that "there is nothing in Wallace's sketch which is not written out much fuller in my sketch copied in 1844" (Burkhardt and Smith 1992, p. 117). Several years later, on May 14th, 1864, Hooker called Darwin's attention to a recent writing of Wallace's (Wallace 1864) in which the latter did not claim any authorship whatsoever in the theory –he uses there expressions such as "Mr. Darwin's celebrated theory of natural selection", and "the theory promulgated by Mr. Darwin". This perplexed Hooker who said "I am struck [...] with his negation of all credit or share in the Natural Selection theory" (Hooker 1864). Darwin's reaction was to write to Wallace and admonish him thus: "You ought not [...] speak of the theory as mine; it is just as much yours as mine." (Burkhardt 2001, p. 216)

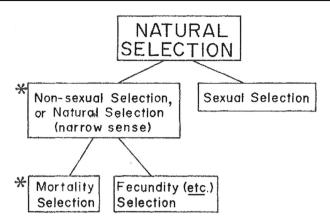


Fig. 1 Reproduction of Endler's hierarchical schema (Endler 1986, p. 9)

called "historicist revolt" in Philosophy of Science, such as Kuhn (1970) and Lakatos (1976, 1978), among others. The most conspicuous representatives of Historicism may differ in many respects, but concur at least in arranging the plurality of elements constituting scientific theories in a hierarchical or multi-level array. This pattern has been taken up and refined in the framework of later meta-theories, such as the so called "structuralist view of theories" (Balzer et al. 1987; Sneed 1971).

This hierarchical approach has been employed for the analysis of numerous theories from the empirical sciences, including in particular the theory of natural selection. In this respect the works of Endler (1986) and Tuomi (1981) deserve mention (for similar hierarchical approaches, see Barbadilla 1990; Cadevall i Soler 1988; Darden and Cain 1989; Reif et al. 2000). Let us begin our journey by briefly presenting Endler's reconstruction.

In *Natural Selection in the Wild*, Endler (1986, pp. 3–15) acknowledges the stratified character of the theory and distinguishes two varieties of natural selection, sexual and non-sexual (see Fig. 1). Note that for Endler not every case of natural selection involves the struggle for existence. Instead, *survival* is but one case among others of the theory of non-sexual selection, a case he dubs "restricted natural selection".⁴

On Endler's view, the theory of sexual selection is included in the structure of the theory of natural selection. Endler even discusses the possibility of sexual selection being a type of natural selection (Endler 1986, p. 11; 1992). Darwin on occasions doubted this kind of inclusion. Wallace, on the other hand, apparently never viewed it as a possibility. Most probably, this attitude contributed to natural selection being thought of as opposed to sexual selection for a long time; a view with which Endler disagrees, and so do we. (We will return to this later.)⁵

⁴ Endler is not alone in this. Many other authors claim that *fitness* can be determined independently of survival (Ginnobili 2010, 2016; Gould 1976; Kutschera 2003, p. 354; Lerner 1959; Naylor and Handford 1985; Wassermann 1978). On the other hand, Lennox and Wilson think that, for Darwin, the struggle for existence is necessary for natural selection to occur (Lennox and Wilson 1994).

⁵ The same idea can be found in other authors. For example, Castrodeza (1988, pp. 182–183), Bateman (1948), Mayr (1972), Ghiselin (1969, p. 242), Gruber (1974, pp. 87–88), Thornhill and Alcock (1983),

As we go down this hierarchy, the applicability of the theory to specific cases increases. What lies behind this structure is that every case of, say, selection by fecundity will also be a case of non-sexual selection and of natural selection (but not a case of sexual selection).

Juha Tuomi, in turn, in his Structure and Dynamics of Darwinian Evolutionary Theory (Tuomi 1981)—a follow-up of his previous works published in collaboration with Tuomi and Haukioja (1979a, b)-holds that an adequate representation of the theory involves what he calls, partially following Bunge and Lakatos, a "multi-level dynamic model", featuring interconnected substructures that include different levels of abstraction. Tuomi identifies the highest portion as the hard core from which no predictions can be extracted, and is, in consequence, unfalsifiable. But one can obtain observational consequences from the more "specific" theories derived from this core, and these do possess empirical content and are, in fact, falsifiable. In the same vein, Tuomi and Haukioja hold that individual theories are not in a vacuum, but in combination with other theories, which suggests that they might not be on the same level. That being the case, the upper levels contain very abstract theories, not directly testable through predictions. These authors explicitly claim that the so-called Darwinian theory is in fact such a complex of theories (cf. Tuomi and Haukioja 1979a, pp. 1-2). Following a classical line, they think the derivation relation between the hard core and its lower-level theories is deductive (cf. Tuomi 1981, pp. 22–23, 27).

In the 1981 paper, Tuomi presents a diagram of the theory of natural selection (TNS):

Tuomi (1981, pp. 28–30) ends with a Kuhnian interpretation of his proposal: during the stage of normal science a pragmatic dogmatism predominates that manifests itself in the preservation of the highest, most abstract parts of the theory (Tg), while admitting criticism of the lower, accidental and more specific parts (Ts). A central, essential portion of the theory remains in effect irrefutable. Nevertheless, Tuomi rightly points out that we should not identify TNS with that restricted portion.

This kind of hierarchical perspective has turned out to be enormously fertile. Lately it has been used to elucidate old debates, but also to more novel debates in philosophy of science—in particular, debates that involve the theory of natural selection. An example is Díez and Lorenzano (2013) where this approach has proven useful in taking a stand on philosophical and historical controversies.

To agree with our conclusions, we insist, the reader need not adhere globally to these perspectives. Rather, he should grant us its adequacy in at least this: scientific theories can be represented as arranged in different levels—some of which are more important or essential than others for the identity of their respective theories—, and include laws of different degrees of generality and abstraction that depend on the particular layer in which they are located. It is this distinction between essential and non-essential constituents what enables us to see theories as malleable entities, with a history; things which are born develop and die, changing from the cradle to the grave,

Footnote 5 continued

Spencer and Masters (1992), Dobzhansky et al. (1977, p. 118), Ayala (1995, pp. 80–82) and especially Ghiselin (1997), p. 226.

but nevertheless preserving their identity all along. We imagine that any historian of science will wish to preserve this intuition.

As can be seen, we do not address the interesting and necessary question regarding which specific meta-theoretical perspective proves most adequate for the clarification of scientific constructs in general, or even of this one in particular. In 1987, Biology and Philosophy dedicated an entire volume to discussing this matter (even focusing on evolutionary theories) and there the contenders were the Syntactic and the Semantic Views (cf. Blanco 2011). Although we have defended a model-theoretic approach for the reconstruction of scientific theories in other works (Blanco 2012; Ginnobili 2010, 2012, 2016) and we do in fact employ tools and concepts from the aforementioned Structuralist View (a member of the semantic family) in this very paper, the reader may subscribe to our arguments independently of his preferences on this issue. The reason for this is that we only make an assumption that both approaches share (or might as well do) in this post-Kuhn era, i.e., that scientific theories are "made of" (or "are represented by", if the reader so prefers) a collection of elements arranged in hierarchical order. For our purposes all that is needed is that the reader grant that theoretical constructs possess this kind of structure, which is as compatible with syntactic approaches (as in the case of Tuomi, Haukioja or Endler) as it is with semantic approaches (as in Cadevall i Soler or Barbadilla).

3.2 Reconstruction of the theory of natural selection in *OS* (1859) as a hierarchical structure

In OS Darwin starts his exposition of the theory of natural selection with this statement:

Let it be borne in mind in what an endless number of strange peculiarities our domestic productions, and, in a lesser degree, those under nature, vary; and how strong the hereditary tendency is. [...] Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. (Darwin 1859, pp. 80–81)

Many authors concur in seeing in this section the structure of the theory and, therefore, have proposed informal reconstructions based on it (among other sources, Flew 1959; Ghiselin 1969, p. 46; Huxley and Asúa 1942; Klimovsky 1994, pp. 178–182; Mayr 1982, pp. 479–481; 1991, p. 72; 2001, p. 116).

Notwithstanding this coincidence, these works exhibit deficiencies that render them inadequate (Ginnobili 2010; Kitcher 1993, pp. 34–37). Darwin himself seems to have regarded this more as an argument for the theory rather than as a brief exposition of

it (Darwin 1883, vol. I, p. 9; Gayon 1998, p. 23). But, what is still worse, there is no brief explicit formulation of the theory of natural selection in any of his writings.

This scenario is not particularly grim. It is frequent not to find this kind of shortcut when it comes to reconstruction. On the other hand, and luckily this time, it is possible to capture the structure of any given theory by abstracting its constituent elements from its applications.⁶

If we turn first to its *explanandum*, it is clear that, at least for Darwin, this theory intends to explain how living organisms acquire the traits that enable them to cope with their environments (we just mention the acquisition of adaptations, but of course there are more elements in the set of *explananda*, such as the origin of species itself). What is revealing is that the different answers, though varied in some respects, all have the same structure.

For example, how is it that a given population of partridges acquired a feather color that helps them to avoid their predators? (Darwin 1859, pp. 84–85). Darwin's answer is the following application of TNS:

Those partridges that possess a color that blends better with their environment in the eyes of their predators improve their survival, thereby improving their differential reproductive success whenever the traits involved can be inherited.

We can find other applications of TNS that also resort to an improvement in survival due to mimicry (Darwin 1859, p. 197). In later editions, Darwin offers explicit examples, such as certain caterpillar that closely resembles the branches it feeds on (Darwin 1872, p. 182). If we search for what is common to both applications we can take a step towards a more abstract law:

Those organisms that manage to blend better with their environment in the eyes of their predators improve their survival, thereby improving their differential reproductive success whenever the traits involved can be inherited.

But, of course, not every case of improvement in survival involves mimicry. In another instance of the theory, Darwin uses the case of the structure of a proboscis in nectar-feeding insects, where improvements in survival are due to improvements in feeding (Darwin 1859, p. 94):

Those organisms whose traits perform their functions more adequately improve their survival, thereby improving their differential reproductive success whenever the traits involved can be inherited.

In these three applications, though in some sense different, we can dissect *at least* three elements in common:

- 1. The heritable trait that performs a function more effectively.
- 2. Differential reproductive success.

⁶ Darwin himself told Lyell (in his letter of June 18th, 1858) that "all the labour" in his Book "consists in the application of the theory" (Burkhardt and Smith 1992, p. 107). As a matter of fact, one of us performed just this task by going through every kind of practical application of the theory that we can find in *OS*, identifying both what they all share and their differences (Ginnobili 2010, 2012, 2016).

3. What connects the trait and reproductive success (*in these three cases*) is an improvement in survival.

We should note that, just as different traits may prove adequate for performing one or more of multiple functions, the reasons why these traits lead to differential reproductive success is not always the same. In fact, this can already be seen in the cases just presented, because, though all of them involve survival, in the first two we have mimicry while in the third we have an improvement in the ability to obtain food.

If we turn our attention to other sorts of cases presented by Darwin, we find that an improvement in survival (for whatever reasons) is but one of the many ways the functional trait may lead to favorable differential reproduction. (Here we clearly come close to Endler's view.)

For example, Darwin acknowledges that reproduction may be improved by means of sexual selection, as happens in mating (Darwin 1859, p. 88). The law-like statement would then be, *mutatis mutandi*:

Roosters with spurs that are more effective for fighting other roosters tend to mate more, thus improving their success in differential reproduction⁷

Of course, mating can be achieved by means different from overcoming a rival of the same sex in a fight. Sexual selection can be thought of from the point of view of the opposite sex, as occurs in numerous cases in which the females' choice of mate does not involve any fight between the males, but rather courting protocols such as construction of potential nests, display of attractive feathering, gift offerings, etc. The subject of sexual selection will be a crucial point for our purposes when we evaluate its place—or rather, its absence—in Wallace's thought, in Sect. 4.

In OS this opposition is still more explicit:

⁷ To conceiving sexual selection as a form of natural selection may be considered controversial. If natural selection is confined to what relates to survival, it is clear that sexual selection then constitutes a different construct. In fact, it could be argued that sometimes Darwin himself seemed to regard them as different for that very reason. See, for instance, this statement from the 1842 text:

Besides selection by death, in bisexual animals (illegible) the selection in time of fullest vigour, namely struggle of males; even in animals which pair there seems a surplus $\langle ? \rangle$ and a battle, possibly as in man more males produced than females, struggle of war or charms. Hence that male which at that time is in fullest vigour, or best armed with arms or ornaments of its species, will gain in hundreds of generations some small advantage and transmit such characters to its offspring. (Darwin 1909a, p. 10)

[[]Sexual Selection] depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring. *Sexual selection is, therefore, less rigorous than natural selection*. (Darwin 1859, p. 88, our emphasis)

In these terms, sexual selection will have applications that exclude those of natural selection. On the other hand, and this is crucial, putting these discussions aside, it is enough for our purposes that the use of the same concepts be recognized in all the proposals we review here. This clue will enable us to see unity in the diversity of theories, as Endler and Tuomi did. Our treatment will be justified, we hope, later on in this section.

Even when in these cases the explanation does not involve improvements in survival or in the ability to attract mates, they still have terms in common with the preceding applications of TSN. For example (Darwin 1859, p. 92):

Plants that produce flowers more attractive for insects tend to improve their fecundity, thus improving their success in differential reproduction.

The list of cases could go on. However, for our purposes it is enough to stress that in *all* the different applications of the theory, with no exception, we find the same concepts, except that they are specified differently. This preservation in every application is essential for the reconstruction. A link is retained between functional traits and reproductive success, even if it adopts different forms in the different specializations.

What constitutes this link is a concept that varies across Darwin's different applications of the theory and that is crucial for explanatory purposes. In fact, it is because this initially abstract concept receives different interpretations or particularizations according to the case being analyzed, that it was possible for Darwin to provide explanations that, notwithstanding their diversity, can all be included within the framework of one and the same theory.⁸

If we call the concept in question "*aptitude*" (we deliberately chose this term in order to avoid the use of "fitness", which could be confusing),⁹ the fundamental law—that is, the law that rules every application of the theory, despite the variety we have shown—can be expressed by the following statement:

Individuals with traits that perform a given function more efficiently improve their aptitude, thus improving, if the trait can be inherited, their success in differential reproduction.

From a theoretical item that includes this quasi-abstract law, one can obtain other theoretical elements that constitute the successive specializations/specifications that enrich the global structure of the theoretical construct. This relation of specialization is reflexive, non-symmetric and transitive, and no deduction is involved in it because new additional information is progressively included as we go down the theoretical structure. (This is an important difference between our approach and Tuomi's in so far as the latter talks about deductive inferences in his hierarchical reconstruction). The different interpretations of the concept of *aptitude* are made explicit in the respective special laws that specify it, bringing out both the unifying and the explanatory power of the theory.

⁸ We insist: the connection between the trait that is adequate for the environment and success in differential reproduction may be due to different reasons: either an improvement in survival, or an improvement in mating, or an improvement in the ability to attract pollinators, etc., all of which may, in turn, be due to different causes.

⁹ This terminological choice may be strange for the reader. It is a predicament hard to overcome. We either choose terms are not typically used to talk about natural selection, which makes the text harder to read; or, rather, we opt for terms that are more familiar and run the risk of being misinterpreted or of upsetting those who use these terms in a different way. This is a consequence of the fact that in this discussion the number of concepts involved outruns the number of terms to express them.

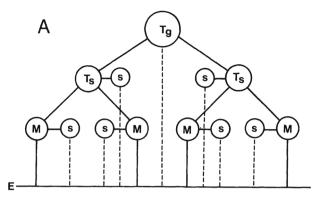


Fig. 2 Reproduction of the diagram in Tuomi (1981). Initials correspond to Mario Bunge's terminology. Tg generic theory, Ts specific theory, M theoretical model, s auxiliary assumption, E empirical level. In conjunction with certain theoretical components (not to be confused with any element from structuralism) these "auxiliary assumptions" make it possible to deduce new theories. For instance, from the theory of natural selection in its generic version (Tg) plus Mendelian genetics (s) we can obtain the more specific Neodarwinian theory (Ts)

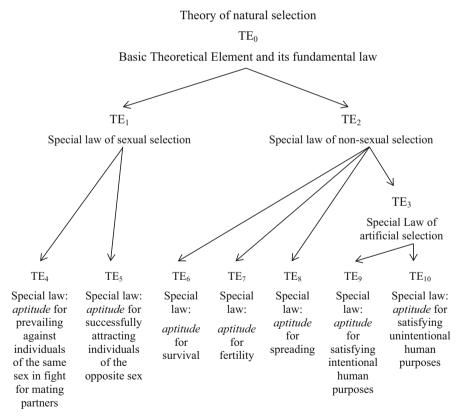


Fig. 3 Hierarchical structure of the theory of natural selection. The nodes represent the theoretical elements and the lines the relation of specialization. Adapted from (Ginnobili 2010, 2016)

The result shown in Fig. 3 resembles the structures in Figs. 1 and 2: it includes not only all the cases mentioned so far, but also some others Darwin identified, such as, for example, both methodical and non-methodical artificial selection, either intentional or unintentional (Darwin 1868, Chapter 20; 1859, pp. 33–43), which were so important for his argument (Evans 1984; Ruse 1975; Sterrett 2002).¹⁰

(It can be argued that an unintentional human action cannot be a case of artificial selection. If we were to exclude it, it would be harder to think of artificial selection as a case of natural selection. In that case, Wallace's silence on artificial selection, which we discuss below, would be justified. Our decision is not influenced by these consequences, but by the intention of following Darwin's intuition.)¹¹

As we go down the hierarchy, the domain of application of each theoretical element T_n gets increasingly more restricted, since the theory gains in empirical content as its concepts become more specific. (Clearly, this increase in information helps us to avoid confusing the relation of specialization with deduction.)

We should note that in Fig. 3, the theoretical element of sexual selection (TE_1) and the theoretical element of artificial selection (TE_3) are different from the theoretical element of natural selection as restricted to survival (TE_6) . All three, however, are part of the same theory: the theory of natural selection, whose basic theoretical element (TE_0) includes a fundamental law that is valid for all applications of all theoretical elements of the theory.

3.3 The unifying power of Darwin's theory

There are (at least) two ways in which we can say that Darwinian theories have unifying power, both present in Darwin's texts:

a. It has unifying power in the sense that the theory assembled disciplines and/or theories that would otherwise appear as unconnected (Ruse 1998), such as—among others—paleontology, biogeography, embryology, comparative anatomy and functional biology. As early as the second edition of OS (1860), Darwin wrote that this is what makes his theory especially convincing:

I cannot believe that a false theory would explain, as it seems to me that the theory of natural selection does explain, the several large classes of facts above specified. (Darwin 1860, pp. 480–481).

¹⁰ Note that the theory of artificial selection can also be thought of as different from that of natural selection restricted to survival. This is hinted at in several passages from Darwin himself in later editions of *OS* (Darwin 1872, pp. 39, 80–81, 137–138), and from many commentators that follow him on this when they present these theories as being in competition (Beer 2001, p. 166; Karlin and Carmelli 1975; Minvielle 1981; Nicholas and Robertson 1980; Secord 1981) and deserving separate treatment. Even though the relationship between artificial selection and natural selection is undoubtedly debatable, here we assume the position that artificial selection can be judged as a case of natural selection (Álvarez 2010; Brandon 1978, 1990, p. 13, Gayon 1998, pp. 54–59; Campbell 1984, pp. 149–152; Richards 2014; Wilner 2006; Ginnobili 2011; among others). For our purposes, it is sufficient to know that that relationship has been discussed in Darwin's version of the theory, and that it is absent in Wallace's version because he explicitly denied that possibility (at least in the treated works).

¹¹ We thank an anonymous reviewer for pointing this out to us.

And in the sixth and last edition (1872):

It can hardly be supposed that a false theory would explain, in so satisfactory a manner as does the theory of natural selection, the several large classes of facts above specified. (Darwin 1872, p. 421)

If we understand "unifying" in this sense, Wallace would stand on a par with Darwin once again. In fact, already in the Sarawak manuscript, a text that, as we will see, is "merely" transformist and still makes no mention whatsoever about natural selection, he wrote:

(My law) connects together and renders intelligible a vast number of independent and hitherto unexplained facts. (Wallace 1855)

b. It has unifying power in the sense that it has an abstract guiding principle (Moulines 1982, pp. 88–107) that allows for heterogeneous specializations by the specification of the fundamental concepts in its framework. This is the sense in which Kitcher said that particle classical mechanics have unifying power (Kitcher 1993, Chapter 2). In the layered conception of theories we have proposed, we see this capacity through the possession of a general principle that is valid for all the specific applications of the theory. In the case of classical mechanics, this is possible by specifications of the concept of force; in the case of the theory of natural selection by specification of the concept we have called "*aptitude*".

We have seen that this characteristic (the specifications of the guiding principle of the theory) can be found in Darwin's version of the theory. Later we will see this is not the case in Wallace's, which will be a key difference for our purposes.

4 The theory of natural selection in Darwin's early writings

The fact that Wallace shared with Darwin correspondence in which he denied the special creation of species as evidence that the transformist doctrine of the latter might have leaked out of his inner circle. It cannot be coincidence that among the various renowned naturalists in the community, Wallace would choose no other than Darwin to send his more controversial writings. This suggests that Wallace might have known of Darwin's transformism. However, they did not discuss the issue, as far as we know from the surviving correspondence between them.

The fact that Darwin possessed Wallace's two essays prior to 1859 was what raised doubts about the originality of the ideas found in *OS*. For this reason, it is imperative for our purposes to examine those writings of Darwin that concern natural selection and were conceived before any communication with Wallace about it (that is, prior to 1858, assuming what is, as far as we know, universally accepted: that Darwin's evolutionism dates from long before 1855, when he learnt about the Sarawak manuscript).

In his first essay of 1842, Darwin presents natural selection using the same argument we saw in *OS*:

If variation be admitted to occur occasionally in some wild animals, [...] if we admit such variations tend to be hereditary, [...] if we admit selection is steadily

at work, and who will doubt it, when he considers amount of food on an average fixed and reproductive powers act in geometrical ratio. If we admit that external conditions vary [...] then, if no law of nature be opposed, there must occasionally be formed races, [slightly] differing from the parent races. [...] it is impossible to say we know the limit of variation. And therefore with the [adapting] selecting power of nature, infinitely wise compared to those of man, $\langle I \text{ conclude} \rangle$ that it is impossible to say we know the limit of races. (Darwin 1909a, pp. 20–21)

On the other hand, it can be observed that the structure of the fundamental law present in the 1844 manuscript is essentially the same as the one we have formulated above:

Those individuals with the lightest forms, longest limbs, and best eyesight [...] would be slightly favored, let the difference be ever so small, and would tend to live longer and to survive during that time of the year when food was shortest; they would also rear more young, which young would tend to inherit these slight peculiarities. (Darwin 1909b, p. 92)

The same structure can also be found in the famous letter to the American botanist Asa Gray, dated September 5th 1857 (and read by Lyell in the *Linnean Society* on July 1858):¹²

Considering the infinitely various ways, beings have to obtain food by struggling with other beings, to escape danger at various times of life, to have their eggs or seeds disseminated &c. &c, I cannot doubt that during millions of generations individuals of a species will be born with some slight variation profitable to some part of its economy; such will have a better chance of surviving, propagating, this variation, which again will be slowly increased by the accumulative action of Natural selection. (Burkhardt and Sydney 1990, p. 445)

In these writings, and this is of vital importance for our view, natural selection is already a general mechanism that not always involves an improvement in survival. For instance, in the early 1842 writings we come across artificial selection:

Man selects only $\langle ? \rangle$ what is useful and curious—has bad judgment, is capricious—grudges to destroy those that do not come up to his pattern,—has no [knowledge] power of selecting according to internal variations,—can hardly keep his conditions uniform,—[cannot] does not select those best adapted to the conditions under which $\langle the \rangle$ form $\langle ? \rangle$ lives, but those most useful to him. (Darwin 1909a, p. 4)

And in his letter to Gray:

It is wonderful what the principle of Selection by Man, that is the picking out of individuals with any desired quality, and breeding from them, and again picking

¹² Gray is one the few people we are aware of that had come to know Darwin's transmutationist ideas before 1858 directly from Darwin's own mouth or pen. Others were, chronologically, Joseph Hooker; Leonard Jenyns; Charles Lyell; William Fox; George Thwaites; Samuel Woodward; and James Dana (see Costa 2013, p. 229; Kottler 1985; Porter 1993). On the other hand, Darwin personally explained in detail the theory of natural selection to Lyell, Hooker and Thomas Huxley.

out, can do. [...] There must have been, also, a kind of unconscious selection from the most ancient times–namely in the preservation of the individual animals (without any thought of their offspring) most useful to each race of man in his particular circumstances. [...] I am convinced that intentional and occasional selection has been the main agent in making our domestic races. [...] Man by this power of accumulating variations adapts living beings to his wants. [...] Now suppose there was a being, who did not judge by mere external appearance [...] who should go on selecting for one end during millions of generations, who will say what he might not effect! (Burkhardt and Sydney 1990, p. 445)

But there is more. In the 1844 essay, we find references to sexual selection (in the two versions already indicated in the reconstruction of the theory according to *OS*), with an exemplary case of application:

These struggles [of the males for the females] are generally decided by the law of battle; but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock-thrush of Guiana. (Darwin 1909b, pp. 92–93)

And also selection by spreading of seeds:

If the number of individuals of a species with plumed seeds could be increased by greater powers of dissemination within its own area [...], those seeds which were provided with ever so little more down, or with a plume placed so as to be slightly more acted on by the winds, would in the long run tend to be most disseminated; and hence a greater number of seeds thus formed would germinate, and would tend to produce plants inheriting this slightly better adapted down. (Darwin 1909b, p. 92)

To summarize, already in Darwinian texts prior to 1858 it is possible to identify a version of the theory that involves varied applications that are not confined to survival, but also include artificial selection (intentional and non-intentional) and sexual selection.

But, what can we say about Wallace's proposal?

5 The theory of natural selection in Wallace (1858)

A quick glance at the text that came to Darwin's hands in 1858 (Wallace 1858) is enough to appreciate an important difference between these authors concerning the role assigned to artificial selection:

One of the strongest arguments which have been adduced to prove the original and permanent distinctness of species is, that varieties produced in a state of domesticity are more or less unstable, and often have a tendency, if left to themselves, to return to the normal form of the parent species. [...] It will be observed that this argument rests entirely on the assumption that varieties occurring in a state of nature are in all respects analogous to or even identical with those of domestic animals, and are governed by the same laws as regards their permanence or further variation. But it is the object of the present paper to show that this assumption is altogether false, that there is a general principle in nature which will cause many varieties to survive the parent species, and to give rise to successive variations departing further and further from the original type. (Wallace 1858, p. 62)¹³

The reasons why Wallace rejects the analogy between natural and artificial selection are probably double.¹⁴ On the one hand, to do so would open the door to intentional and/or purposeful action in nature that he thought to be inappropriate.¹⁵ On the other hand, as Costa (2013) points out, maybe Wallace is considering Lyell's anti-evolutionary writings, and that is why he stresses reversion in artificial selection—without human intervention, the varieties obtained will revert to the original form, exactly one of the arguments Lyell used against Lamarck—forcing himself to weaken or even reject the analogy with natural selection, because he thinks the creative power of the former is limited whilst that of the latter is responsible for many (in Wallace, probably all) features of biodiversity. (It should be taken into account that Lyell was the final addressee of the manuscript.)

Darwin, on the contrary, meant to strengthen the analogy between artificial and natural selection. 16

We can interpret Darwin's personal and almost obsessive study of the creative effect (limited on account of the ephemeral nature of our efforts, but genuine nonetheless) of artificial selection in pigeons as a direct application of the theory of natural selection insofar as the former constitutes a special case of the latter (Darwin 1868, vol. 1, p. 3).¹⁷ Here we find, then, a first difference by omission: Wallace leaves artificial selection out of the picture in his version of the theory. Since we have not been able

¹³ In a letter to Lyell, Darwin himself wrote that Wallace and him "differ only that I [Darwin] was led to my views from what artificial selection has done for domestic animals" (Burkhardt and Smith 1992, p. 117).

¹⁴ Let us remember that for this reason Wallace urges Darwin to substitute the expression "natural selection" for "survival of the fittest". Darwin ended up following his colleague's advice. In the fifth edition of *OS* he wrote:

I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection. But the expression often used by Mr. Herbert Spencer of the Survival of the Fittest is more accurate, and is sometimes equally convenient. (Darwin 1869, p. 72)

Wallace's proposal was delivered (once again) by correspondence, in a letter dated July 2nd 1866. As Darwin admits, Herbert Spencer (1820–1903) coined the expression, more specifically, in his *The Principles of Biology* of 1864 (Spencer 1864). Darwin adopted the Spencerian language in this fifth edition of *OS* and in the sixth one. However, he never dropped "natural selection" altogether, but preserved it, using both expressions interchangeably up to the end (Darwin 1872, pp. 80, 102, 134–135, 180, 471) (Adopting this terminology is inadequate for multiple reasons. To mention an oft-quoted one, it was precisely this formulation that drove many authors to (wrongly) declare the theory to be unfalsifiable on account of circularity.)

¹⁵ It is well known that in later writings Wallace advocated for teleological versions of evolution, specifically for the appearance of humans (Carmo and Martins 2006; Fichman 2001; Levit and Polatayko 2013; Wallace 1869a, 1903, 1910, 1913), a topic that exceeds our present purposes.

¹⁶ Cf. (Kutschera 2003), where we can find this and other interesting differences between Darwin's and Wallace's theoretical proposals. On account of our approach, we only pick up two: the difference in how they treat natural selection and Wallace's omission of sexual selection, about which we will speak later in this section.

¹⁷ Note what Darwin claims at the beginning of his longer work *The Variation of Animals and Plants underDomestication*:

to show the stability of the varieties obtained by breeders, it is not proper to take what they do as analogous to what, as he assumes, nature produces.

Artificial selection is not, however, the only missing piece. Wallace does not contemplate sexual selection either.

Let us recall that, in our schema (Fig. 3), the theory of artificial selection, the theory of sexual selection, and the theory of natural selection as restricted to survival, are component parts of the structure of the theory of natural selection as it appears in *OS*, and none of the former should be confused with the latter. We have shown that the three theories are applications that not only share a similar structure, but also resort to specifications of *the same* conceptual framework. This shows us a sense, both interesting and relevant for our discussion, in which we can speak of them as applications of *one and the same* theory.

Much has been written about this omission. It launched one of the several controversies that distanced Wallace's thought from Darwin's from 1859 onwards. A thorough discussion of this issue exceeds our goals. Let us just say that, in time, Wallace gradually accepted with more or less reluctance, other applications conceived by Darwin, especially those pertaining to sexual selection, albeit with great reservations as to their domain of application. Additionally, it cannot be ignored that in a work as late as *Darwinism*, Wallace still thinks that natural selection is restricted mainly (solely?) to cases that involve an improvement in survival, even though his presentation is far more elaborate than it was in 1858.

So far we have been reviewing Wallace's omissions in relation to Darwin's proposal—we refer the reader to Ruse (2013), and again Kutschera (2003) for other differences. Now, as regards to what Wallace does contemplate, it is most interesting to see to what extent his own exposition resembles or is even identical to Darwin's. It is surprising and remarkable that he presents the idea based on the same reflections and, even, sometimes using the same expressions. See, for instance, this paragraph:

The life of wild animals is a struggle for existence. [...] The possibility of procuring food during the least favourable seasons and of escaping the attacks of their most dangerous enemies, are the primary conditions, which determine the existence both of individuals and of entire species. These conditions will also determine the population of a species. [...] The numbers that die annually must be immense; and as the individual existence of each animal depends upon itself, those that die must be the weakest [...], while those that prolong their existence can only be the most perfect in health and vigor—those who are best

Footnote 17 continued

No doubt man selects varying individuals, sows their seeds, and again selects their varying offspring. [...] Man, therefore, may be said to have been trying an experiment on a gigantic scale; and it is an experiment which nature during the long lapse of time has incessantly tried. Hence, it follows that the principles of domestication are important for us. (Darwin 1868, vol. 1, p. 3; cf. Wilner 2006)

Just as breeders intervene positively selecting those traits which will be useful for their ends and they are interested in preserving, thereby creating in relatively few generations products that satisfy their practical or aesthetic agenda, in an analogous manner nature "chooses", unintentionally but not randomly, "creating" and preserving new varieties for different reasons (Darwin 1859, Chapters 1–2). Again, Darwin attributes a greater creative power to the selective force of nature than he does to artificial selection.

able to obtain food regularly, and avoid their numerous enemies. It is, as we commenced by remarking, "a struggle for existence", in which the weakest and least perfectly organized must always succumb. (Wallace 1858, pp. 56–57)

The similarities with Darwin are numerous. Nevertheless, we have to emphasize one more time that in the 1858 text natural selection *always* works by means of an improvement in survival. The particular cases are two.

First, survival due to an ability to avoid predators or one to obtain resources (TE₁₂ in Fig. 4):

An antelope with shorter or weaker legs must necessarily suffer more from the attacks of the feline carnivore; the passenger pigeon with less powerful wings would sooner or later be affected in its powers of procuring a regular supply of food; and in both cases the result must necessarily be a diminution of the population of the modified species. If, on the other hand, any species should produce a variety having slightly increased powers of preserving existence that variety must inevitably in time acquire superiority in numbers. (Wallace 1858, p. 58)

Second, survival due to camouflage (TE₁₁ in Fig. 4):

Even the peculiar colours of many animals, especially insects, so closely resembling the soil or the leaves or the trunks on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints may have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest*. (Wallace 1858, p. 61, author's emphasis.)¹⁸

Even though we only have cases relating to survival (TE₆ both in Figs. 3 and 4), it is possible to abstract the concepts involved. When we apply here the same criteria of explication we employed before, the similarities with Darwin stand out. In fact, in this paragraph it is possible to identify the same (or very similar) components we find in OS:

- 1. A trait present in an organism performs a function (here mentioned generically)
- 2. This function improves the *aptitude* of the organism in a particular activity (in this case, survival), which leads to
- 3. an advantage for the organism in differential reproduction.

On the one hand, the coincidence even in the use of terms is extraordinary.¹⁹ On the other, the theory Wallace formulated is less general and has less unifying force than Darwin's, since it is restricted in all cases to just one (no more and no less) of the several kinds of applications contemplated by Darwin. Wallace envisaged and presented in his work only the *restricted* version of natural selection (as Endler called natural selection)

¹⁸ Note that camouflage can be useful to survival both for escaping predators—what Wallace wrote about and food supply—what Wallace omitted—(cf. Dfez and Lorenzano 2013, 2015).

¹⁹ So extraordinary that it can hardly be attributed to chance. Perhaps a historiographical analysis of their interaction before 1858 could shed light to an explanation (see Kottler 1985). Notwithstanding this, we should remember that these coincidences surprised Darwin himself (cf. note 3).

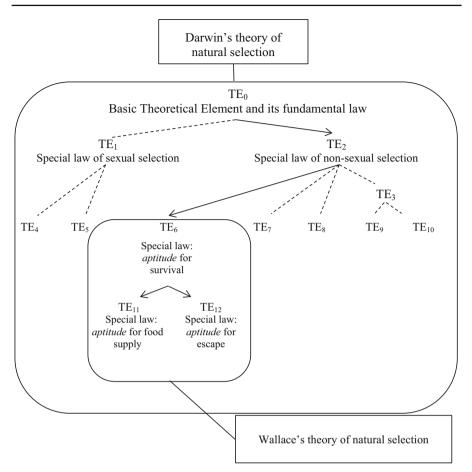


Fig. 4 The theoretical elements we can find in Wallace's theory of natural selection can be seen a substructure of the one of Darwin's (cf. Fig. 3). As in Fig. 3, the nodes represent the theoretical element and the lines the relation of specialization

relating to survival), either by procurement of food, flight or mimicry. Ultimately, he only discusses cases relating to survival (see Fig. 4).

Although Wallace's text is brief and leaves out many cases characterized in OS, the similarity in reasoning on the issue discussed by both is simply stunning. However, because of having a more restricted concept of *aptitude*, Wallace's theory of natural selection does not have the unifying power we can find in Darwin's.

6 Conclusions

1. As one might suspect, the systematic approach regarding the way both authors introduce the theory does not necessarily go hand in hand with an approach based on temporal priority, because we can find that one version is more complete than the other independently of chronological issues. In the mature version of the theory

of natural selection according to Darwin, as it appears in *OS*, and from a systematic study based on a hierarchical perspective of scientific theories, we can discern a more complex and ramified structure than the one we find in Wallace's Ternate manuscript.

- 2. Notwithstanding conclusion (1), it is possible to identify the fundamental elements of this theoretical construct in early Darwinian texts, prior to 1858. Even in these instances we can identify a concept of *aptitude* that, though maybe not as sophisticated as the one presented in *OS*, is not restricted merely to survival.
- 3. The Ternate manuscript presents a version of the theory that, despite its coincidence with Darwin's version in presenting *the same fundamental elements*, is less rich because of assuming that the link between the utility of traits and reproductive success occurs constantly and invariably through (diverse improvements in) survival. Although, as in Darwin, survival may occur for many reasons such as improvements in procurement of food, improvements in the ability to hide from predators, improvements in defense, etc. Unlike Darwin, Wallace makes no references to sexual selection (and, consequently, to its several forms), there is no mention of fecundity or spreading of seeds, and there is even an explicit claim that artificial selection is a process distinct from (and opposed to) natural selection.
- 4. There is a sense in which the badge of "co-discoverer" is well deserved by Wallace: the theory in his writings and in Darwin's is the same inasmuch as the same conceptual framework can be abstracted from the works of both authors. Additionally, their proposals turn out to be surprisingly coincident in many of their concrete applications. Notwithstanding all this, in Darwin we find a more complex theoretical construct, with more variants in its applications and with greater unifying power than the one Wallace gave us. Furthermore, in Darwin we can find a more abstract and encompassing law than the one we can find in Wallace.
- 5. By (1)–(4), we believe that "the Darwin-Wallace theory" is a particularly adequate alternative name for the theory of natural selection: it acknowledges the joint authorship (in the sense that both independently devised the essence of one and the same theory), and at the same time it expresses the sense explained here in which Darwin has some priority over Wallace.
- 6. The theory of natural selection and that of the common origin are the most revolutionary theories in the history of biology. Almost invariably, this revolution goes by the name of "Darwinian revolution". Although the co-authorship is arguable with respect to the theory of natural selection, we score a point in favor of the appropriateness of that terminology. Because if, as some (Darwin included) believe, the reason why the theory of natural selection was (and should be) accepted by biologists, lies not so much in its predictive success, but rather in its unifying power, then the credit is all Darwin's. After all, as we saw, unifying power in both senses of that phrase can (at least in 1859) only be found in the Darwinian version of the theory. Yes, both versions put forward a similar "guiding principle", but only Darwin's version can account for a heterogeneous collection of data by means of already special laws, or by postulating new special laws (cf. Díez and Lorenzano 2013; Ginnobili 2010, 2016). Given that the concept we have called "aptitude" admits of different specializations only in Darwin's version of the theory and not in Wallace's one, the unifying power is greater in the former. If this unifying force

(in the second sense we have described in Sect. 3.3) is indeed what drove the scientific community to put its confidence in the theory of natural selection, then this change was brought about by Darwin's version of the theory, not Wallace's. For that reason, even though it can be held that, in essence, the theory of natural selection was invented as much by Wallace as by Darwin, the scientific revolution brought about is, in all fairness, Darwinian.

Acknowledgements We want to thank Roberto Biaggi, Damien Rochford and two anonymous referees for their helpful comments on previous versions of this paper. This research was supported by the research Projects PICT-2014-1741 (ANPCyT, Argentina), Research Program "Philosophy and History of Science" PUNQ, 1719/11 (UNQ, Argentina), and 32/15 255 (UNTREF, Argentina).

References

Álvarez, J. R. (2010). La selección natural: lenguaje, método y filosofía. Endoxa, 24, 91-122.

- Ayala, F. J. (1995). Origen y Evolución del Hombre. Madrid: Alianza Editorial.
- Balzer, W., Moulines, C. U., & Sneed, J. D. (1987). An architectonic for science: The structuralist program. Dordrecht: Reidel.
- Barbadilla, A. (1990). La estructura de la teoría de la selección natural. In A. Ruiz & M. Santos (Eds.), Temas Actuales de Biología Evolutiva. Barcelona: UAB.
- Barrett, P. H., Gautrey, P. J., Herbert, S., Kohn, D., & Smith, S. (Eds.). (1987). *Charles Darwin's notebooks*. New York: Cornell University Press.
- Bateman, A. J. (1948). Intra-sexual selection in Drosophila. Heredity, 2(3), 349-368.
- Beddall, B. G. (1968). Wallace, Darwin, and the theory of natural selection: A study in the development of ideas and attitudes. *Journal of the History of Biology*, 1(2), 261–323.
- Beddall, B. G. (1972). Wallace, Darwin, and Edward Blyth: Further notes on the development of evolution theory. *Journal of the History of Biology*, 5(1), 153–158.
- Beddall, B. G. (1973). Notes for Mr. Darwin: Letters to Charles Darwin from Edward Blyth at Calcutta: A study in the process of discovery. *Journal of the History of Biology*, 6(1), 69–95.
- Beddall, B. G. (1988). Darwin and Divergence: The Wallace connection. *Journal of the History of Biology*, 21(1), 1–68.
- Beer, G. (2001). La evolución de la novela. In A. Fabián (Ed.), Evolución. Sociedad, ciencia y universo (pp. 157–182). Barcelona: Tusquets Editores.
- Blanco, D. (2011). Las teorías científicas nacen como respuesta a problemas de la experiencia. Una objeción a Paul Thompson. Ludus Vitalis, 19(35), 113–130.
- Blanco, D. (2012). Primera aproximación estructuralista a la Teoría del Origen en Común. Ágora, 31(2), 171–194.
- Blyth, E. (1835). An attempt to classify the varieties of animals, with observations on the marked seasonal and other changes which naturally take place in various british species, and which do not constitute varieties. *Magazine of Natural History*, 8, 40–53.
- Bock, W. (2009). The Darwin-Wallace Myth of 1858. Proceedings of the Zoological Society, 62(1), 1–12.
- Brackman, A. C. (1980). A delicate arrangement: The strange case of Charles Darwin and Alfred Russel Wallace. New York: Times Books.
- Brandon, R. (1978). Adaptation and evolutionary theory. Studies in History and Philosophy of Science, 9, 181–206.
- Brandon, R. (1990). Adaptation and environment. Princeton: Princeton University Press.
- Brooke, J. (1984). Just before the origin: Alfred Russel Wallace's theory of evolution. New York: Columbia University Press.
- Brooks, J. (1969). Re-assessment of A. R. Wallace's contribution to the theory of organic evolution. Year Book 1968, Am. Phil. Sci (pp. 539–535).
- Brooks, J. (1972). Extinction and the origin of organic diversity. *Transactions of the Connecticut Academy* of Arts and Sciences, 44, 19–56.
- Bueno Hernández, A., & Llorente Bousquets, J. (2003). El pensamiento biogeográfico de Alfred Russel Wallace. México DF: UNAM.

- Burkhardt, F., Porter, D. M., Dean, S. A., White, P. S., & Wilmot, S. (Eds.). (2001). The correspondence of Charles Darwin, v. 12: 1864. Cambridge: Cambridge University Press.
- Burkhardt, F., & Smith, S. (Eds.). (1992). The correspondence of Charles Darwin, v. 7: 1858–1859. Cambridge: Cambridge University Press.
- Burkhardt, F., & Sydney, S. (Eds.). (1990). The correspondence of Charles Darwin, v. 6: 1856–1857. Cambridge: Cambridge University Press.
- Burstyn, H. L. (1975). If Darwin wasn't the Beagle's naturalist, Why was he on board? *The British Journal for the History of Science*, 8(1), 62–69.
- Cadevall i Soler, M. (1988). La estructura de la teoría de la evolución. Barcelona: Universitat Autònoma de Barcelona.
- Camerini, J. R. (1993). Evolution, biogeography, and maps: An early history of Wallace's line. *Isis*, 84(4), 700–727.
- Campbell, J. H. (1984). An organizational interpretation of evolution. In D. J. Depew & B. H. Weber (Eds.), *Evolution at a crossroads: The new biology and the new philosophy of science* (pp. 133–167). Cambridge: MIT Press.
- Caponi, G. (2009). Definitivamente no estaba ahí. Scientiae Studia, 17(32), 55-73.
- Castrodeza, C. (1988). Ortodoxia darwiniana y progreso biológico. Madrid: Alianza Editorial.
- Costa, J. T. (2013). Engaging with Lyell: Alfred Russel Wallace's Sarawak law and ternate papers as reactions to Charles Lyell's principles of geology. *Theory in Biosciences*, 132(4), 225–237.
- Costa, J. T. (2014). Wallace, Darwin, and the origin of species. Cambridge: Harvard University Press.
- Darden, L., & Cain, J. (1989). Selection type theories. Philosophy of Science, 56, 106-129.
- Darwin, C. R. (1839). Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle. London: Colburn.
- Darwin, C. R. (1859). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: John Murray.
- Darwin, C. R. (1860). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (2nd ed.). London: John Murray.
- Darwin, C. R. (1861). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (3rd ed.). London: John Murray.
- Darwin, C. R. (1868). The variation of animals and plants under domestication. London: John Murray.
- Darwin, C. R. (1869). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (5th ed.). London: John Murray.
- Darwin, C. R. (1872). The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life (6th ed.). London: John Murray.
- Darwin, C. R. (1883). The variation of animals and plants under domestication. New York: D. Apleton and Co.
- Darwin, C. R. (1909a). Essay of 1842. In F. Darwin (Ed.), The foundations of the origin of species. Two essays written in 1842 and 1844 (pp. 1–53). Cambridge: Cambridge University Press.
- Darwin, C. R. (1909b). Essay of 1844. In F. Darwin (Ed.), The foundations of the origin of species. Two essays written in 1842 and 1844 (pp. 57–255). Cambridge: Cambridge University Press.
- Darwin, C. R. (1958). The autobiography of Charles Darwin 1809–1882. With the original omissions restored. Edited and with appendix and notes by his grand-daughter Nora Barlow. London: Collins.
- Díez, J. A., & Lorenzano, P. (2013). Who got what wrong? Fodor and Piattelli on Darwin: Guiding principles and explanatory models in natural selection. *Erkenntnis*, 78(5), 1143–1175.
- Díez, J. A., & Lorenzano, P. (2015). Are natural selection explanatory models a priori? *Biology and Philosophy*, 30(6), 887–889.
- Dobzhansky, T., Ayala, F. J., Stebbins, G. L., & Valentine, J. W. (1977). Evolution. San Francisco: W. H. Freeman and Company.
- do Carmo, V. A., & Martins, L. A.-C. P. (2006). Charles Darwin, Alfred Russel Wallace e a seleção natural: um estudo comparativo. *Filosofia E História Da Biologia*, 1(1), 335–350.

Eiseley, L. (1958). Darwin's century: Evolution and the men who discovered it. New York: Barnes & Nobles.

- Eiseley, L. (1979). Darwin and the mysterious Mr. X. New York: Harvest Books.
- Endler, J. A. (1986). Natural selection in the wild. Princeton: Princeton University Press.
- Endler, J. A. (1992). Natural selection: Current usages. In E. FoxKeller & E. A. Lloyd (Eds.), Keywords in evolutionary biology (pp. 220–224). Cambridge: Harvard University Press.
- Evans, L. T. (1984). Darwin's use of the analogy between artificial and natural selection. *Journal of the History of Biology*, *17*(1), 113–140.

- Fichman, M. (2001). Science in theistic contexts: A case study of Alfred Russel Wallace on human evolution. Osiris, 16, 227–250.
- Fichman, M. (2004). An elusive victorian: The evolution of Alfred Russel Wallace. Chicago: University of Chicago Press.
- Flew, A. G. N. (1959). The structure of Darwinism. New Biology, 28, 25-44.
- Gayon, J. (1998). Darwinism's struggle for survival: Heredity and the hypothesis of natural selection. Cambridge studies in philosophy and biology. Cambridge: Cambridge University Press.
- Ghiselin, M. T. (1969). The triumph of the Darwinian method. Berkeley: University of California Press.
- Ghiselin, M. T. (1997). *Metaphysics and the origin of species. SUNY series in philosophy and biology.* Albany: State University of New York Press.
- Ginnobili, S. (2010). La teoría de la selección natural darwiniana. Theoria, 25(1), 37-58.
- Ginnobili, S. (2011). Selección artificial, selección sexual, selección natural. Metatheoria, 2(1), 61–78.
- Ginnobili, S. (2012). Reconstrucción estructuralista de la teoría de la selección natural. Ágora Papeles de Filosofía, 31(2), 143–169.
- Ginnobili, S. (2016). Missing concepts in natural selection theory reconstructions. *History and Philosophy* of the Life Sciences, 38(3), 8.
- Gould, S. J. (1976). Darwin's untimely burial. Natural History, 85, 24-30.
- Gould, S. J. (1987). An urchin in the storm. New York: Norton & Company Inc.
- Gruber, H. E. (1974). Darwin on man: A psychological study of scientific creativity. Chicago: University of Chicago Press.
- Hodge, M. J. (1977). The structure and strategy of Darwin's 'long argument'. British Journal for the History of Science, 10(3), 237–246.
- Hodge, M. J. (1983a). Darwin and the laws of the animate part of the terrestrial system (1835–1837). Studies in History of Biology, 6, 1–106.
- Hodge, M. J. (1983b). The development of Darwin's general biological theorizing. In D. S. Bendall (Ed.), *Evolution: From molecules to men* (pp. 43–62). Cambridge: Cambridge University Press.
- Hodge, M. J. (1985). Darwin as a lifelong generation theorist. In D. Kohn (Ed.), *The Darwinian heritage:* A centennial retrospect (pp. 207–243). Princeton: Princeton University Press.
- Hodge, M. J. (2010). Darwin, the Galapagos and his changing thoughts about species origins: 1835–1837. In *Proceedings of the California Academy of Sciences*, Series 4, vol. 61, Supplement II, No. 7, pp. 89–106.
- Hodge, M. J., & Kohn, D. (1985). The immediate origins of natural selection. In D. Kohn (Ed.), *The Darwinian heritage: A centennial retrospect* (pp. 185–206). Princeton: Princeton University Press.
- Hooker, J. D. (1864). Hooker to Darwin, 14 May 1864. https://www.darwinproject.ac.uk/entry-4494. Retrieved 15 Oct 2015.
- Hossfeld, U., & Olsson, L. (2013). The prominent absence of Alfred Russel Wallace at the Darwin anniversaries in Germany in 1909, 1959 and 2009. *Theory in Biosciences*, 132(4), 251–257.
- Huxley, J., & de Asúa, F. (1942). Evolution: The modern synthesis. London: George Allen and Unwin.
- Karlin, S., & Carmelli, D. (1975). Some population genetics models combining artificial and natural selection pressures. *Theoretical Population Biology*, 7, 94–148.
- Kitcher, P. (1993). The advancement of science: Science without legend, objectivity without illusions. New York: Oxford University Press.
- Klimovsky, G. (1994). Las desventuras del conocimiento científico. Buenos Aires: A-Z Editora.
- Kottler, M. (1985). Charles Darwin and Alfred Russell Wallace: Two decades of debate over natural selection. In D. Kohn (Ed.), *The Darwinian heritage* (pp. 367–431). Princeton: Princeton University Pess.
- Krimbas, C. B., & Krimbas, C. B. (2004). On fitness. Biology and Philosophy, 19, 185–203.
- Kuhn, T. (1970). The structure of scientific revolutions (2nd ed.). Chicago: University of Chicago Press.
- Kutschera, U. (2003). A comparative analysis of the Darwin–Wallace papers and the development of the concept of natural selection. *Theory in Biosciences*, *122*(4), 343–359.
- Kutschera, U. (2008). Darwin-Wallace principle of natural selection. Nature, 453(7191), 27.
- Kutschera, U., & Hossfeld, U. (2013). Alfred Russel Wallace (1823–1913): The forgotten co-founder of the Neo-Darwinian theory of biological evolution. *Theory in Biosciences*, 132(4), 207–214.
- Kutschera, U., & Niklas, K. (2004). The modern theory of biological evolution: An expanded synthesis. *Naturwissenschaften*, 91, 255–276.
- Lakatos, I. (1976). Proofs and refutations. Cambridge: Cambridge University Press.
- Lakatos, I. (1978). The methodology of scientific research programmes: Philosophical papers (Vol. 1). Cambridge: Cambridge University Press.

- Lennox, J., & Wilson, B. (1994). Natural selection and the struggle for existence. Studies in History and Philosophy of Science, 25(1), 65–80.
- Lerner, I. M. (1959). The concept of natural selection: A centennial view. *Proceedings of the American Philosophical Society*, 103(2), 173–182.
- Levit, G., & Hossfeld, U. (2011). Darwin without borders? Looking at generalised Darwinism through the prism of the hourglass model. *Theory in Biosciences*, 130(4), 299–312.
- Levit, G., & Polatayko, S. (2013). At home among strangers: Alfred Russel Wallace in Russia. *Theory in Biosciences*, 132(289–297), 292–293.
- Lloyd, D., Wimpenny, J., & Venables, A. (2010). Alfred Russel Wallace deserves better. *Journal of Bio-sciences*, 35(3), 339–349.
- Lyell, C. (1830). Principles of geology. London: John Murray.
- Malthus, T. R. (1798). An essay on the principle of population. London: John Murray.
- Mayr, E. (1972). Sexual selection and natural selection. In B. C. Campbell (Ed.), Sexual selection and the descent of man (pp. 1871–1971). Chicago: Aldine Publishing Company.
- Mayr, E. (1982). The growth of biological thought. Cambridge: Harvard University Press.
- Mayr, E. (1991). One long argument. Cambridge: Harvard University Press.
- Mayr, E. (2001). What evolution is. New York: Basic Books.
- McKinney, H. L. (1966). Alfred Russel Wallace and the discovery of natural selection. *Journal of the History of Medicine and Allied Sciences*, XX, I(4), 333–357.
- McKinney, H. L. (1969). Wallace's earliest observations on evolution: 28 December 1845. Isis, 60(3), 370–373.
- McKinney, H. L. (1972). Wallace and natural selection. New Haven: Yale University Press.
- Michaux, B. (1966). Alfred Russel Wallace, biogeographer. In C. H. Smith & G. Beccaloni (Eds.), Natural selection and beyond: The intellectual legacy of Alfred Russel Wallace. Oxford: Oxford University Press.
- Minvielle, F. (1981). Natural selection opposing artificial selection: A two-locus deterministic simulation. Genetics, 98, 231238.
- Moore, J. (1997). Wallace's Malthusian moment: The common context revisited. In B. Lightman (Ed.), Victorian science in context (pp. 290–311). Chicago: University of Chicago Press.
- Moulines, C. U. (1982). Exploraciones metacientíficas. Estructura, desarrollo y contenido de la ciencia. Madrid: Alianza.
- Naylor, B. G., & Handford, P. (1985). In defense of Darwin's theory. BioScience, 35(8), 478-484.
- Nicholas, F. W., & Robertson, A. (1980). The conflict between natural and artificial selection in finite populations. *Theoretical and Applied Genetics*, 56(1–2), 57–64.
- Porter, D. (1993). On the road to the origin with Darwin, Hooker, and Gray. Journal of the History of Biology, 26(1), 1–38.
- Recker, D. (1990). There's more than one way to recognize a Darwinian: Lyell's Darwinism. *Philosophy* of Science, 57(3), 459–478.
- Reif, W., Junker, T., & Hossfeld, U. (2000). The synthetic theory of evolution: General problems and the German contribution to the synthesis. *Theory in Biosciences*, 119(1), 41–91.
- Richards, R. A. (2014). Darwin's experimentalism. Endeavour, 38(3-4), 235-245.
- Ruse, M. (1975). Charles Darwin and artificial selection. Journal of the History of Ideas, 36(2), 339–350.
- Ruse, M. (1998). *Taking Darwin seriously: A naturalistic approach to philosophy*. New York: Prometheus Books.
- Ruse, M. (2013). Charles Robert Darwin and Alfred Russel Wallace: Their dispute over the units of selection. *Theory in Biosciences*, 132(4), 215–224.
- Schwartz, J. (1974). Charles Darwin's debt to Malthus and Edward Blyth. Journal of the History of Biology, 7(2), 301–318.
- Secord, J. A. (1981). Nature's fancy: Charles Darwin and the breeding of pigeons. Isis, 72(2), 163-186.
- Secord, J. A. (2000). Victorian sensation. Chicago: The University of Chicago Press.
- Slotten, R. A. (2004). The heretic in Darwin's court: The life of Alfred Russel Wallace. New York: Columbia University Press.
- Smith, C. (2015). Alfred Russel Wallace and the road to natural selection, 1844–1858. Journal of the History of Biology, 48(2), 279–300.
- Sneed, J. D. (1971). The logical structure of mathematical physics. Dordrecht: Reidel.
- Spencer, H. (1864). The principles of biology (Vol. 1). London: William and Norgate.

- Spencer, H. G., & Masters, J. C. (1992). Sexual selection: Contemporary debates. In E. F. Keller & E. A. Lloyd (Eds.), *Keywords in evolutionary biology* (pp. 294–301). Cambridge: Cambridge University Press.
- Stauffer, R. C. (Ed.). (1975). Charles Darwin's natural selection; being the second part of his big species book written from 1856 to 1858. Cambridge: Cambridge University Press.
- Sterrett, S. G. (2002). Darwin's analogy between artificial and natural selection: How does it go? Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 33(1), 151–168.
- Sulloway, F. (1982). Darwin's conversion: The Beagle voyage and its aftermath. Journal of the History of Biology, 15, 325–96.
- Sulloway, F. (2009). Tantalizing tortoises and te Darwin-Galápagos legend. Journal of the History of Biology, 42, 3–31.
- Thornhill, R., & Alcock, J. (1983). The evolution of insect mating systems. Cambridge: Harvard University Press.
- Tuomi, J. (1981). Structure and dynamics of Darwinian evolutionary theory. *Systematic Zoology*, 30(1), 22–31.
- Tuomi, J., & Haukioja, E. (1979a). An analysis of natural selection in models of life-history theory. *Savonia*, *3*, 9–16.
- Tuomi, J., & Haukioja, E. (1979b). Predictability of the theory of natural selection: An analysis of the structure of the Darwinian theory. Savonia, 3, 1–8.
- van Wyhe, J. (2016). The impact of A. R. Wallace's Sarawak law paper reassessed. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 60, 56–66.
- Wallace, A. R. (1853). Narrative of travels on the Amazon and Rio Negro, with an account of the native tribes, and observations on the climate, geology, and natural history of the Amazon Valley. London: Reeve & CO.
- Wallace, A. R. (1855). On the law which has regulated the introduction of new species. Annals and Magazine of Natural History, 16, 184–196.
- Wallace, A. R. (1858). On the tendency of varieties to depart indefinitely from the original type. Journal of the Proceedings of the Linnean Society of London, 3, 53–62.
- Wallace, A. R. (1864). The origin of human races and the antiquity of man deduced from the theory of natural selection. *Anthropological Society of London*, 2, 158–186.
- Wallace, A. R. (1869a). Review of principles of geology and elements of geology, by Charles Lyell. Quarterly Review, 126, 359–394.
- Wallace, A. R. (1869). The Malay Archipelago: The land of the Orang-Utan and the bird of paradise. A narrative of travel, with studies of man and nature. London: Macmillan & Co.
- Wallace, A. R. (1870). Contributions to the theory of natural selection. A series of essays. London: Macmillan & Co.
- Wallace, A. R. (1880). Island life: Or, the phenomena and causes of Insular Faunas and Floras, including a revision and attempted solution of the problem of geological climates. London: Macmillan & Co.
- Wallace, A. R. (1889). Darwinism: An exposition of the theory of the theory of natural selection with some of its applications. London: Macmillan & Co.
- Wallace, A. R. (1891). Natural selection and tropical nature: Essays on descriptive and theoretical biology. London: Macmillan & Co.
- Wallace, A. R. (1898). The wonderful century; its successes and its failures. London: Swan Sonnenschein & Co.
- Wallace, A. R. (1903). Man's place in the Universe: A study of the results of scientific research in relation to the unity or plurality of worlds. London: Chapman & Hall.
- Wallace, A. R. (1905). My life: A record of events and opinions. London: Chapman & Hall.
- Wallace, A. R. (1908). Wallace acceptance speech on receiving the Darwin-Wallace medal. In Linnean Society of London (Ed.), *The Darwin-Wallace Celebration held on thursday, 1st July, 1908, by the Linnean Society of London*. London: Burlington House.
- Wallace, A. R. (1909). Note on the passages of Malthus's "principle of population" which suggested the idea of natural selection to Darwin and myself. The Darwin–Wallace celebration held on Thursday. 1st July 1908, by the Linnean Society of London. London: Longmans Green & Co.
- Wallace, A. R. (1910). The world of life: A manifestation of creative power, directive mind and utimate purpose. London: Chapman & Hall.
- Wallace, A. R. (1913). Social environment and moral progress. London: Cassell & Co.

Wassermann, G. D. (1978). Testability of the role of natural selection within theories of population genetics and evolution. *The British Journal for the Philosophy of Science*, 29(3), 223–242.

Wilner, E. (2006). Darwin's artificial selection as an experiment. *Studies in History and Philosophy of Science Part C*, 37(1), 26–40.