

Missing concepts in natural selection theory reconstructions

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Received: 6 April 2015 / Accepted: 26 June 2016
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Abstract The concept of fitness has generated a lot of discussion in philosophy of biology. There is, however, relative agreement about the need to distinguish at least two uses of the term: ecological fitness on the one hand, and population genetics fitness on the other. The goal of this paper is to give an explication of the concept of ecological fitness by providing a reconstruction of the theory of natural selection in which this concept was framed, that is, based on the way the theory was put to use in Darwin's main texts. I will contend that this reconstruction enables us to account for the current use of the theory of natural selection. The framework presupposed in the analysis will be that of metatheoretical structuralism. This framework will provide both a better understanding of the nature of ecological fitness and a more complete reconstruction of the theory. In particular, it will provide what I think is a better way of understanding how the concept of fitness is applied through heterogeneous cases. One of the major advantages of my way of thinking about natural selection theory is that it would not have the peculiar metatheoretical status that it has in other available views. I will argue that in order to achieve these goals it is necessary to make several concepts explicit, concepts that are frequently omitted in usual reconstructions.

Keywords Ecological fitness · Natural selection theory · Darwin · Metatheoretical structuralism · Population genetics

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1 Introduction

There is a long-running discussion about the concept of *fitness* in biology and the philosophy of biology, and by now a widespread agreement that it is necessary to distinguish at least two concepts of “fitness”. On the one hand, as I will explain in Sect. 2 of this paper, there is a concept that comes from population genetics, which is linked to the notion of the selection coefficient and can be determined by the statistical and probabilistic methods that are typical of this discipline. On the other hand, there is a second concept that I will call “ecological fitness”, following Rosenberg and Bouchard (2009). Though the nature of this concept of ecological fitness is less clear, at this point we can advance that it is independent of and historically prior to population genetics and related to ecological or physiological “causes” of the differences in reproductive success.

In this paper, I will continue the discussion that arose from the attempt to explicate the concept of ecological fitness. A central issue of my explication is to give an adequate account of the way in which the theory of natural selection unifies its extremely heterogeneous set of applications with the help of the abstract concept of fitness. The problem is that there is no specific “physical” property that is uniquely relevant to the determination of ecological fitness and hence could provide a basis for unification (Brandon 1990; Rosenberg 1983). There are two main ways of dealing with this problem. One way is to appeal to the concept of supervenience (Rosenberg 1978). Fitness supervenes on the different physical properties of organisms that are relevant to ecological fitness. Another common way of dealing with this problem is to appeal to the propensity interpretation of fitness (Mills and Beatty 1979; Brandon 1978). In this view propensities for fitness are sustained by physical properties. I will present these two positions in Sect. 3.

My strategy in this paper will not be to criticize these positions but rather to offer a better solution to the problem they tried to tackle (the problem that ecological fitness cannot be linked to a unique set of physical properties). Both aforementioned positions have the undesirable consequence of turning fitness into a peculiar concept whose application seems to differ from the way in which fundamental concepts are normally applied in paradigmatic scientific theories. The main point of this paper is to argue that by appealing to the right analytical tools, in this case provided by metatheoretical structuralism, it is possible to show that the way of applying the concept of ecological fitness is no different from the application of usual theoretical concepts. Moreover, the fact that applications of fitness are heterogeneous is related to the unifying power of natural selection theory.

As the concept of ecological fitness acquires meaning within the framework of natural selection theory (NST from hereon) I will provide a reconstruction of NST based on Charles Darwin’s texts in Sect. 4. The main intention of this paper is to discuss these questions within the framework of contemporary biology. The reason why I choose to present the issue by examining the way in which Darwin thought about natural selection is twofold: on the one hand, it will be—as I will try to show—both fruitful and clarifying in the face of the complexity of the discussion within contemporary philosophy of biology; on the other hand, my choice results

from the historiographic interest of showing the validity of Darwinian ideas in the present.

In my reconstruction of NST I will presuppose the analytical framework of metatheoretical structuralism derived from the work of Joseph Sneed (1971)—also called “Sneedian structuralism.” Instead of presenting my structuralist reconstruction in the formal way that is typical of this approach, however, I will merely appeal to some notions of structuralism and analyze NST in an informal way. In particular, my interest relies on the structuralist notions of *specialization*, *specification* and *theory-net*, and its distinction between *fundamental* and *special laws*. These notions, which find their origin in Kuhnian thought—specifically in the distinction between generalization-sketches and specific laws (Kuhn 1970a, p. 465)—, have been developed and clarified within the structuralist program. In the structuralist view of theories special laws cannot be deduced from fundamental laws (as it is in the classical view of theories) since special laws have more empirical content and new information; they rather arise from the specification of abstract concepts that are present in fundamental laws. This insight will be crucial in order to understand that the heterogeneity of applications of the concept of ecological fitness is not peculiar but rather typical of fundamental concepts in unifying theories.

As I have said, this approach stems from the writings of Sneed (1971), but it has been developed by the work of many philosophers of science. There are several more recent works that present the approach (Balzer et al. 1987; Moulines 1982, 1991; Balzer and Moulines 1996; Díez and Lorenzano 2002). Moreover, it is worth noting that metatheoretical structuralism has proven to be fruitful in dealing with biological theories (e.g., Lorenzano 1995, 2007, 2014; Casanueva 2011; Ginnobili 2010, 2011a, 2012a; Federico 2009; Barbadilla 1990; Balzer and Dawe 1997; Casanueva 1997; Mendez and Casanueva 2006; Lorenzano et al. 2007; Lorenzano 2010; O’Lery 2010; Blanco 2012; Lorenzano 2012; Mendez and Casanueva 2012; Alleva et al. 2012; O’Lery 2012; Díez and Lorenzano 2013).

Metatheoretical structuralism is one of the semantic conceptions of scientific theory, according to which a theory is not identified with a set of statements but through a collection of models (Winther 2015). Metatheoretical structuralism is a sophisticated tool which has become increasingly complex through the analysis and reconstruction of theories from different disciplines, constantly enriching its own conceptual apparatus. My intention is not to give a full presentation, but only briefly outline the concepts used in this paper.

One of the most important influences on metatheoretical structuralism is the work of Thomas Kuhn. In particular, what Kuhn writes about disciplinary matrices, nomic generalizations, and exemplars (Kuhn 1970a p. 465, b Postscript). According to Kuhn, in theories like Classical Particle Mechanics there are no laws in the traditional way (i.e., universal and exceptionless statements that logically imply the special laws of the theory). For example, the formula that represents Newton’s second law of motion, $f = ma$, is a “scheme” that takes on specific forms in the treatment of particular puzzles. This idea has been elaborated in detail in the context of structuralism. The fundamental law of a theory is a highly abstract element that cannot be empirically tested in isolation, but only through special laws. Special laws arise from the fundamental law not by deduction but by specialization. This relation

specifies the concepts of the fundamental law, increasing the content and adopting a similar but less abstract form. The fundamental law and all of its specializations are a theory-net. For example, the theory-net of Classical Particle Mechanics arises from the second law of Newton. This is the top unifying nomic component. The different branches arise through different specifications of the concept of *force*. In one branch we have all the special laws that speak about space-dependent forces, and in another branch we have the velocity-dependent forces. Then the space-dependent branch specializes into direct and indirect space-dependent, etc. At the bottom of every branch we have a totally specific law that applies to the particular puzzles that Kuhn talked about: pendula, gravitation, inclined planes, etc.

It is worth noting that there is a change in the reconstructive strategy—with regard to the classical scientific theory conception in which a theory is a set of statements related by deductive relations—which underlies the notion of theory-net, and which is partly the reason why structuralism has succeeded in the task of reconstructing scientific theories. In the classical conception, the question was, *From what fundamental laws are all applications of this theory deduced?* This question is difficult, or even impossible, to answer, and it probably explains in part the lack of success in reconstructing theories from this perspective. The question we try to answer from structuralism is, *What do all the different applications of a theory have in common?* As we shall see in the case that interests us, it is possible to answer this question, and though it is not always easy, that answer allows us to present the theory properly.

The reconstruction of Darwinian NST that I will offer allows me to point out two features that are still relevant in reconstructions of current NST—despite the fact that NST may have suffered many modifications throughout its history. The first feature is that, in order to give a complete reconstruction of selectionist explanations, it is necessary to make explicit concepts that are frequently omitted in other available reconstructions. The second feature is that NST consists of a net of special laws—emerging from the diverse specifications of the fitness concept—from which the unifying character of the theory emerges. Both features allow me to elaborate what I consider a more accurate answer to the main problem that this paper deals with: the problematic fact that the concept of ecological fitness is specified by different particular properties of organisms but cannot be defined by any of them. I will present this answer in Sect. 5.

This discussion will allow us to understand the role of NST in current evolutionary biology, showing how it is a genuine theory, different and independent from population genetics, and moreover allowing us to strengthen the point made by those who consider that NST complements the statistical-probabilistic studies of population genetics, by identifying the ecological causes of differences in selection coefficients (Bouchard 2011; Peacock 2011; Rosenberg 1994; Glymour 2006).

2 Two kinds of fitness?

Several authors have maintained that there are two kinds of fitness. Elliott Sober, for example, distinguishes two ways of conceiving of natural selection: one framed by population genetics, and another which specifies the ecological conditions that

produce differences in reproductive success; this corresponds to two ways of calculating fitness, by its consequences in terms of reproductive success, or by the physical properties that cause fitness (Sober 1993, pp. 13–59). Mohan Matthen and André Ariew distinguish between vernacular and predictive fitness (Matthen and Ariew 2002). The first would be based on the abilities of organisms to survive and reproduce, and the second would be the statistical measure of evolutionary change, the expected rate of increase (normalized relative to others) of a gene, a trait, or an organism's representation in future generations. Ariew and Richard Lewontin distinguish, in turn, between Darwinian fitness, which is characterized as an inexact metaphor of how the organism *fits* within its environment, as opposed to reproductive fitness, which is mathematically calculated in population genetics (Ariew and Lewontin 2004). Massimo Pigliucci and Jonathan Kaplan distinguish between informal and formal fitness and, consequently, between informal and formal natural selection (Pigliucci and Kaplan 2006, pp. 17–31). The underlying idea, again, is analogous. Informal fitness concerns the relation between a trait and the environment and how that affects the reproductive success of the organism that possesses it. Formal fitness is a statistical property of populations that is defined from the average growth rate of subpopulations distinguished by the possession of a variation of a trait. Finally, in the entry corresponding to “fitness” in *The Stanford Encyclopedia of Philosophy*, Rosenberg and Bouchard distinguish between ecological fitness and population genetics fitness.¹ The first concerns the ability of the organism to solve design problems, whereas the second concerns genetic reproduction rates (Rosenberg and Bouchard 2009). I do not intend to claim that these distinctions always presuppose exactly the same concepts, but that all of them have at least a “family resemblance”. Each of them distinguishes between a qualitative version close to Darwin's thought, and a quantitative version that arises from the work of population geneticists.

Once this distinction is made, there is a tendency to consider that population genetics fitness provides a more exact, quantitative version of ecological fitness. The assumption behind this idea is that natural selection is defined solely based on the difference of success rates that different organisms enjoy in differential reproduction. If things were so, population genetics—by enabling us to determine quite precisely under certain assumptions that the genic frequency in a population is not as expected (by appealing to the Hardy–Weinberg equilibrium)—would be sufficient to allow us to quantify the action of natural selection.

Thus, for instance, in his popular textbook on evolution Douglas Futuyama claims: “if alleles differ in their replacement rates, their frequencies may change. This phenomenon is called ‘selection’” (Futuyma 1986, pp. 86–87). On the other hand, and in a different discipline, the renowned historian and philosopher of science, Jean Gayon says: “[with the discovery of Hardy and Weinberg] natural selection is no more a fundamental principle, but a parameter that measures one of the many forces of change” (Gayon 1998, p. 321). This seems to be presupposed also by certain authors that give population genetics a fundamental role in

¹ I will use this terminology. The use of “ecological” does not imply that this is a concept of ecology since, as I will show, the ecological fitness is the fitness from NST.

evolutionary biology (Ruse 1973, chapt. 4), and by others who claim to have reconstructed evolutionary theory when, in fact, they only reconstructed population genetics (p.e. Lloyd 1994; Barbadilla 1990; Thompson 1989). It is also an assumption of those who intend to explicate the concept of fitness on the basis of the reconstruction of the theory of evolution as a theory of forces (Sober 1993, pp. 13–59).

Some authors, however, have argued against explicating the concept of fitness solely based on the place it occupies in population genetics. For instance, Bruce Glymour holds that:

Population genetics gives us a set of extraordinarily useful devices for representing frequency changes in natural populations and for describing selection processes. Those uses remain important, even essential, in much of evolutionary and population biology. But, largely as an historical accident, many biologists and nearly all philosophers have over-invested in population genetics, in that, implicitly or explicitly, population genetics is taken to provide the core formal machinery for describing selection processes. (Glymour 2006, p. 388)

Rosenberg, in turn, maintains that:

[...] evolutionary biologists employ the notion of “gene frequencies” as a convenient unit in which to measure the results of various evolutionary forces [...]. Because genes provide the unit of measure of the phenomena to which we apply the theory of natural selection, it is inevitable that population genetics will be central to evolutionary biology. But for the same reason, thermometers are crucial to thermodynamics—they reflect proximate effects we can measure, not ultimate causes. (Rosenberg 1994, pp. 110–111)

In agreement with these opinions, some authors have noted the restrictive character of the population genetics concept of fitness, and have defended instead the ecological concept of fitness, as more explanatory and comprehensive (Bouchard 2011; Peacock 2011). Along similar lines, I will try to show that the concept of ecological fitness, and the theory within which it is framed, are metatheoretically appropriate and that natural selection theory can be adequately presented with independence from population genetics.

In order to explicate the concept of ecological fitness, it is important to show which place this concept occupies in a reconstruction of NST and to analyse the way in which it is applied to intended cases. There is a particular problem facing such reconstructions of NST that present it as a theory independent of population genetics. It is the problem of accounting for the way in which specific traits of organisms contribute to reproductive success. I will address this issue in the next section.

3 Supervenience and propensities

There is a problem that appears repeatedly in reconstructions of NST. It is usually held (i) that there is a relation between fitness and differential reproductive success, (ii) that fitness cannot be reduced to differential reproductive success without facing

the problem of tautology, and (iii) that fitness bears some relation to the particular physical (anatomical, physiological and behavioural) properties or abilities of the organisms. Those who defend the concept of ecological fitness struggle to satisfy the requirements that are implied by all three assumptions. One illustrative case is Rosenberg's account, which presents the relation between fitness and the physical properties of organisms using the concept of supervenience (Rosenberg 1978, 1985, pp. 164–169). Admittedly, if the concept of fitness can explain differences in reproductive success, then it has to involve more than mere differences in reproductive success. Rosenberg wonders how fitness could be related to the physical properties or abilities of organisms (1978, p. 371), if it is possible that two distinct organisms possess the same fitness, but one organism because it evades predators by camouflaging and the other one by flying away. The fitness of organisms is intertwined with a vast number of different physical properties and environmental conditions, which would make it impossible, according to Rosenberg, to establish even a small portion of the nomological connections between a given fitness and all the different properties of organisms, and relations they entertain with other entities in their environment, that can affect it. Sober agrees with Rosenberg on this point (Sober 1993, p. 48). This implies, according to Rosenberg, that fitness can only be measured through reproduction rates. The way Rosenberg secures the explanatory force of NST is by appealing to the concept of supervenience (Davidson 1970):

The concept of “fitness” is supervenient on the manifest properties of organisms, their anatomical, physiological, behavioral, and environmentally relative properties. And this fact alone explains the simultaneous explanatory power and empirical recalcitrance of the concept of fitness. (Rosenberg 1978, p. 372)

This concept makes room for claims that the supervenient properties are not reducible to physical ones, but depend on them insofar as there cannot be two events similar in all physical respects but different with respect to the supervenient property (see also Sober 1993, pp. 47–59).

The problem lies in relating the concept of fitness with reproductive success on one hand, and the physical properties of organisms on the other (Rosenberg 1983, pp. 460–461). This problem is also pointed out by Robert Brandon (1990, pp. 12–13). His solution consists in interpreting fitness as a propensity (Mills and Beatty 1979; Brandon 1978). This prevents the statement “the fitter leave more descendants” from being tautological, because there is a distinction between the offspring actually left and the propensity to leave a certain number of descendants. Success in differential reproduction is explained by the propensity to leave a certain number of descendants of the organisms at hand, the same way solubility explains that a particular amount of salt is dissolved in water (Mills and Beatty 1979, p. 270). Rosenberg is right in having doubts about the explanatory capacity of that statement, which he compares with the explanation of opium causing sleepiness by its *dormitive virtue* (Rosenberg 1985, p. 160), insofar as the mechanism over which the disposition supervenes is not exposed. It is clear, however, that this is considered by Brandon, since the idea of the propensity interpretation of fitness is that the

propensity is sustained by certain physical properties and mechanisms (Brandon 1990, pp. 16–17).

I do not deny that the notion of supervenience might be useful in discussing metaphysical issues about reduction in biology, discussions that are particularly interesting for Rosenberg (Rosenberg and McShea 2008, pp. 96–126). This notion, in effect, makes it possible to assume a physicalist position without having to adopt a reductionist view regarding supervenient properties (Perez 1996). But the question of the relation between the properties of organisms and their success in differential reproduction in the applications that biologists make of NST is not a metaphysical issue. The question at stake is how different concepts—e.g., fitness, reproductive success, and, say, mimicry—relate to each other and interact in explanations given by scientists in their everyday practice. The metaphysical answer cannot, in this way, be either pertinent or satisfactory. I think that metatheoretical structuralism provides a better way to deal with the NST reconstruction and the explication of fitness, since it allows to understand the relation between fitness and physical properties without falling back onto metaphysically problematic concepts.

There are two major views that explicate the concept of fitness and its heterogeneous way of application: the first one appeals to supervenience, and the second one appeals to propensities. They both assume that NST has a peculiar status, which emerges from the alleged strange way of application of ecological fitness. For example, according to many defenders of the propensity interpretation of fitness, the fundamental law of NST (the so called “natural selection principle”) is part of the theory of probability (McShea and Brandon 2010, pp. 108–109; Brandon 1990, p. 21). From my viewpoint, the fundamental law of NST has the same nature like, for example, the fundamental law of classical particle mechanics. This matter is especially relevant since, as it was presented in the preceding section, the metatheoretical adequacy of NST is at stake. In the face of this, it would be valuable to show that it is possible to deal with this matter without implying peculiarities that could reinforce the intuitions of ecological fitness’ detractors.

It is usually maintained that ecological fitness is related to the qualitative manner in which Darwin thought of natural selection. Therefore, my strategy in the next section will consist of presenting a reconstruction of the theory as it was used by Darwin. This will provide a better solution to the problem posed and will additionally disprove the idea that the concept of fitness put forward by Darwin is nothing more than an inexact metaphor (Ariew and Lewontin 2004, p. 348).

4 Darwinian natural selection

4.1 Explanatory domain

The first question to be asked about a theory concerns its domain of application, that is, the kind of phenomena that it is meant to explain. Starting by answering this question will allow us to establish some vocabulary which will, in turn, enable us to distinguish clearly the language introduced by the theory from the language that

describes the phenomenon to be explained, a crucial distinction for the reconstruction of a theory.

What was it that Darwin aimed to explain with natural selection? It is usually said that the purpose of NST is to offer an evolutionary mechanism, that is, a theory that explains the course of evolution. This answer is incomplete. Darwin had many possible evolutionary mechanisms available, such as the effect of environmental conditions, or use and disuse, which in conjunction with the inheritance of acquired traits might cause the transformation of species (Sober 2011, pp. 19–20). If we focus solely on the capacity of the theory of natural selection to explain the transformation of species it is not possible to understand its importance in Darwin's thought or in the *Origin*. What was needed, according to Darwin, was not a mere evolutionary mechanism to explain the course of evolution, but a mechanism that explained the “perfection of structure and coadaptation” of living organisms (Darwin 1859, p. 3), i.e., the mechanisms by which living organisms acquire throughout their phylogenetic development the traits that are suited for survival in their specific environment (Lewens 2007, p. 40, 268; Caponi 2011, p. 1; Dupré 2003, pp. 17–18; Kitcher 1993, pp. 24–25; Gayon 1998, p. 23; Ospovat 1981, p. 60; Ruse 1998, p. 17; Brandon 1990, p. 3; Mayr 1982, p. 481; Cronin 1991, p. 15). Other mechanisms might in Darwin's view explain certain adequacies, but not all (Darwin 1859, p. 3). Lamarckian mechanism, for example, would only be applicable in cases where variation arises from the habit of using or not using certain organs, since the habit of using certain organs or the lack of such use are the source of the increment, or the specialization, or of the detriment and simplification of the altered organs.

This is one of the roles of natural selection. Even if you are persuaded of evolution, it is necessary to possess a mechanism to explain how living organisms seem designed to survive in their environment. Especially when the absence of such mechanism might be—and indeed has been—used to argue against evolution having taken place. Until it was postulated as an evolutionary mechanism, there was no satisfactory way of explaining why certain traits of living organisms seemed designed for the performance of certain functions without resorting to a conscious designer of some kind (Sober 2000, p. 36).

I would like to point out the ambiguity of the term “adaptation” as it is employed in the literature on evolution. In particular, I am interested in distinguishing between two uses (from the many that exist) in its application to traits. The term is often used to refer to traits whose fixation in a population has occurred by a process of natural selection (Sober 2000, p. 85). Darwin, however, often uses the word “adaptation” to speak of those traits that show a certain *adjustment* to the environment. Let's use “adequation” to refer to this adjustment of organisms to their environments, which the theory of natural selection was supposed to explain.²

How does Darwin characterize adequations? This issue is both important and somewhat unclear in the literature on evolution and in Darwin himself. When he refers in a general way to adequations, Darwin points out several features (e.g.,

² Of course, other authors have noted this ambiguity (e.g., West-Eberhard 1994; Burian 1994; Gould and Vrba 1982; Brandon 1990, pp. 39–44). I do not make use of any existing account because later on I will characterize adequations in a way that differs from those available. This characterization will be crucial, since it will influence our view of the very structure of NST.

Darwin 1859, p. 3): perfection of structure, complexity and, what he repeats the most, co-adaptation, which includes co-adaptations between different living organisms, between different parts of the living organism and between the living organism and the living conditions. All these expressions are illustrated in the *Origin* with the exhaustiveness of an accomplished naturalist through examples of the monstrous complexity of the interrelationships between different living organisms.

It is not difficult to see the influence of natural theologians on Darwin's arguments concerning the need for natural selection and the way he conceptualized the phenomenon that both he and they found in need of an explanation. The features discerned by Darwin are the same as those that, according to natural theologians, are evidence of the existence of a designer (Paley 1809, pp. 1–3). Which features of the phenomenon are to be explained? Some, Darwin and William Paley amongst them (Paley 1809, p. 5; Darwin 1859, p. 3), have pointed to the high level of complexity as a key feature of adequations. It would be astronomically improbable that such complex traits were due to known natural causes—the influence of use and disuse and natural selection aside, of course. The wind might shape certain rocks to resemble a human face when seen from certain angles, but it could not shape the faces of the four American presidents on Mount Rushmore, and even less the simplest of the living things we know (Dawkins 1996, p. 5). Another feature of adequations mentioned both by Darwin and Paley is that they have functions. This will be essential to this paper.

I do not intend to find necessary and sufficient conditions for something to count as an adequation in itself, regardless of any theoretical framework whatsoever—I very much doubt that this is possible—, but rather I intend to outline the way adequations are conceptualized in the theory of natural selection. Let us look at an example of the application of the theory by Darwin himself. The set of adequations to be explained is the following:

The giraffe, by its lofty stature, much elongated neck, fore-legs, head and tongue, has its whole frame beautifully adapted for browsing on the higher branches of trees. (Darwin 1872, p. 177)

Which are the adequations to be explained in this case? Certain peculiar traits of the giraffe: the great length of its neck, its head, its front legs and its tongue. Traits that perform their function in an effective manner. Even though Darwin uses complexity in his general characterization of adequations, when applying the NST he only characterizes its domain of application as traits that perform a function in a highly efficient manner. This I will refer to by the expression “adequation” and “adequate trait”. What Darwin wants to explain is, therefore, how the population of giraffes acquired traits that allowed them to feed on the high branches of trees, i.e., traits that perform their function in an effective manner in a particular environment.

4.2 Darwinian explanation of the origin of the adequation

In the different Darwinian explanations of the origin of the different traits we can find the diverse applications of NST. See the famous explanation of the origin of the long traits of the giraffe:

So under nature with the nascent giraffe, the individuals which were the highest browsers and were able during dearths to reach even an inch or two above the others, will often have been preserved; [...] These slight proportional differences, due to the laws of growth and variation, are not of the slightest use or importance to most species. But it will have been otherwise with the nascent giraffe, considering its probable habits of life; for those individuals which had some one part or several parts of their bodies rather more elongated than usual, would generally have survived. These will have intercrossed and left offspring, either inheriting the same bodily peculiarities, or with a tendency to vary again in the same manner; whilst the individuals, less favoured in the same respects, will have been the most liable to perish. (Darwin 1872, pp. 177–178)

Presented in a somewhat more orderly way, the historical explanation offered by Darwin can be rendered as follows:

4.2.1 *Explanans*

1. In the generation G_{0-n} of the population p of giraffes there was some variation in the length of the neck.
2. These differences caused certain differences in the effectiveness with which the trait performed the function of reaching the leaves of the trees in the environment a —this effectiveness might be null in some cases.
3. Giraffes with necks of greater length are more effective in feeding from the higher branches of the trees; they tend to improve their survival and, consequently, their differential reproductive success.
4. Individuals tend to transmit their particular traits to their offspring in some degree.
5. Generation after generation the frequency of the traits that were more effective in the performance of the function increased and so did accordingly the effectiveness with which the function is performed.

4.2.2 *Explanandum*

In G_0 of the population p of giraffes all individuals have long necks that perform the function of reaching the higher branches of trees in their environment with a high rate of effectiveness.

This exposition, that is merely intuitive and sketchy, will serve as a starting point for our analysis since it allows me to draw some essential distinctions.

4.3 Historical NST and non-historical NST

Philip Kitcher intends to reconstruct NST (Kitcher 1993, p. 28) and suggests an explanatory pattern similar to my presentation in Sect. 4.2. To account for this kind

of explanation, among other things, Kitcher elaborates a metatheoretical framework about explanation (Kitcher 1981). Darwin was primarily interested in this historical (in the sense in that appeal to the action of NST along many generations) explanation and many have regarded NST as a historical explanatory device. Another version similar in format to this historical pattern is the one offered by Skipper and Millstein (2005).

I will follow a different path. I will distinguish this historical explanation of the origin of the adequation, whose structure I have just outlined informally and which I will call ‘historical theory of natural selection’—HNST—, from a non-historical theory which I will call ‘non-historical theory of natural selection’—NNST.³ Though I will not discuss the nature of historical explanations in general, in this case the historical explanation of the origin of adequations (based on HNST) appeals to the laws of a non-historical theory (NNST) among other things—we can find it in the statement in point 3 of the *explanans* of HNST in the previous section. But unfortunately these two different—though related—theories are called simply “natural selection”. This ambiguity is responsible for many misunderstandings. Thus, according to many authors the theory of natural selection is not historical (e.g., Lloyd 1994, pp. 2–5), whereas others consider natural selection as an intrinsically historical explanatory device (e.g., Smart 1963, pp. 59–60; Popper 1979, pp. 267–270). This disagreement can be resolved if one considers the ambiguity of the term “natural selection” and distinguishes one theory from the other. In the following section I will informally show the structure of NNST and the differences will become clearer. Just as Kitcher and Skipper & Millstein provide reconstructions of HNST, other authors provide reconstructions of NNST (e.g., Endler 1986; Brandon 1990; Williams 1970; Tuomi and Haukioja 1979). A quick comparison between the corresponding reconstructions of both theories immediately reveals an essential difference between them: they have different *explananda*. As we saw, HNST tries to account for the origin of the adequation. NNST purports instead to explain the differences in reproductive success between organisms that possess certain traits (Brandon 1990, p. 9). HNST must resort to iterations of NNST to account for its *explanandum*.

The distinction between HNST and NNST is extremely useful and can prove relevant in various discussions on natural selection. I will mention two by way of example. One is the dispute concerning the *explanandum* of NST (e.g., Stephens 2007, pp. 114–116; Stegmann 2010). This is because some disagreements are

³ The election of this name, ‘historical theory of natural selection’, presupposes that this historical explanation can be thought of as an application of a theory that can also be reconstructed by means of metatheoretical structuralism. Though I think this can be defended, this discussion will not be addressed here. There is a precedent analogous to the case at hand of two theories that are frequently confused, one of which has the standard form, and the other has a more historical character and iterates the former theory repeatedly and also adds some new concepts. This is the case of the distinction made by Lucía Federico between *metabolic biochemistry* and *biochemistry of the metabolic pathways* (Federico 2009, p. 98). Nevertheless, even if it was not the case and what I have been calling HNST is nothing more than the iteration of NNST, the distinction can still be thought of as two different ways of applying the same theory—instead of two different theories—and the main points of my paper remain unaltered. In any case, to get a better understanding of the historical explanations proposed by Darwin, a reconstruction of NNST—a theory that we find presupposed in his texts—is needed.

provoked by the fact that the disputants having different theories in mind. Another discussion where the distinction is relevant concerns whether natural selection can be considered a mechanism. Skipper and Millsten think it cannot, because, among other things, NST has stages, whereas mechanisms have parts (Skipper and Millstein 2005, p. 339). But they are considering HNST; if they had considered NNST their conclusion might have been different.

In this context, the distinction is extremely relevant since the explication of the concept of ecological fitness will require the reconstruction of NNST, as we shall see in the next section.

4.4 Abstraction of the fundamental law of NNST

Usually, in the fundamental laws of theories, all of a theory's terms appear interrelated (Balzer et al. 1987, p. 19; Lorenzano 2007). In point 3 of the Darwinian explanation of the giraffe's neck—see Sect. 4.2—we find a general factual statement that connects the proper trait with reproductive success in a specific way, and abstracting from this statement we can obtain the fundamental concepts of NNST and the form of its fundamental law.⁴ HNST accounts for its *explanandum* by the iterated application of this law one generation after another.

The special version of the fundamental law of NNST in this particular explanation is:

Longer necked giraffes better perform the function of reaching the higher branches of trees, thus improving their feeding and survival in times of scarcity, and consequently tending to improve, if the longer neck is inheritable, their differential reproductive success.

If we put this application in a more abstract way, we would have something like this:

Organisms that possess a trait r that performs more efficiently its function in a certain environment e tend to improve their survival in e , consequently tending to improve – if r is inheritable – the differential reproductive success in e of these kind of organisms.⁵

Nothing in this statement is superfluous. It is necessary to indicate precisely which function it is that produces the improvement in survival. The function at stake might have been different and it might have affected survival by other means. The long neck, for instance, might have kept predators away. In the analysis of other cases we will see that it is not superfluous either to point out that the connection between reproductive success and the proper trait involves an improvement in survival, since this connection might have been otherwise. The concept that enables us to establish

⁴ The informal application I make of structuralism leads to a presentation of the fundamental law by means of statements, which may cause the reader some confusion given that structuralism is a semantic metatheory. It must be remembered that I am not presenting NNST in a structuralist language, but rather using important concepts of this metatheory in an informal way.

⁵ In Sect. 4.5 I will focus on the notions of function and differential reproductive success and the reason why heritability is introduced in the fundamental law.

such connection is the concept of (ecological) fitness—specified here as survival. The structure of the law and the nature of the concept of fitness, still somewhat indeterminate, will become clearer after a long roundabout in which I will examine different ways in which Darwin applies NNST.

As we shall see, the law we have just abstracted from the case considered is not the fundamental law yet, since, as we shall also see, survival is not involved in every application of NNST. Let us turn our attention to the different kinds of connections between the trait that performs the function more effectively and reproductive success drawing from several examples of applications of NNST that Darwin makes in the *Origin*. My intention is not to show all the ways in which NNST is used by Darwin in the *Origin*, but only the main ones, in order to abstract NNST from its applications. This will help us to better understand the concept of fitness.

4.4.1 Sexual selection

It can be shown that sexual selection is (in structuralist terminology) a “specialization” of NST.⁶ In sexual selection fitness consists in the ability to acquire mates and not in an improvement in survival. Much has been said of the relation between sexual and natural selection, but, as we will see, there is an interesting sense in which it can be claimed that both are applications of one and the same theory; since they have the same structure and the same concepts, even though they are specified differently. The ability to mate can occur by virtue of different reasons:

- Ability to mate by fighting organisms of the same sex; as Darwin states:

Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But in many cases, victory will depend not on general vigour, but on having special weapons, confined to the male sex. A hornless stag or spurless cock would have a poor chance of leaving offspring. Sexual selection by always allowing the victor to breed might surely give indomitable courage, length to the spur, and strength to the wing to strike in the spurred leg [...]. (Darwin 1859, p. 88)

In this case the following factual statement is presupposed:

Cocks with spurs more efficient to fight other cocks, *tend to improve their ability to acquire mates*, consequently tending to improve, if the trait is inheritable, their success in differential reproduction.

- Ability to mate by attracting organisms from the other sex; as Darwin states:

⁶ Although Darwin sometimes presents sexual and natural selection as if they were two distinct mechanisms, he at times also speaks of natural selection in a more comprehensive fashion. I have presented a defense of this point in a previous paper (Ginnobili 2011b). Endler (1986, pp. 11–12), Gayon (1998, pp. 51–54), and Ghiselin (1969, p. 215), amongst others who share this view.

Amongst birds, the contest is often of a more peaceful character. [...] successive males display their gorgeous plumage and perform strange antics before the females, which standing by as spectators, at last choose the most attractive partner. (Darwin 1859, pp. 88–89)

In this case the presupposed factual statement is:

Birds with feathers that are more attractive for the females of their species *improve their ability to acquire mates*, improving in consequence, if the trait is inheritable, their success in differential reproduction.

4.4.2 *Chance to cross*

Those individual flowers which had the largest glands or nectaries, and which excreted most nectar, would be oftenest visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand. (Darwin 1859, p. 92).

In this case there is neither an improvement in survival, as in the case of the giraffe, nor a betterment of the ability to mate. It is a different application. The factual statement presupposed is the following:

Plants that produce flowers that are more attractive for insects *tend to improve their chance to being crossed*, tending consequently to improve, if the trait is inheritable, their success in differential reproduction.

4.4.3 *Artificial selection*

Elsewhere I have argued that we acquire a better understanding of the argument of the *Origin* if artificial selection—the kind of selection in which humans intervene—is considered a case of natural selection (Ginnobili 2011b).⁷ I will not present those arguments again here. I will simply show how artificial selection can be presented as a specialization of the fundamental law of NNST.

Artificial selection can be divided in two kinds:

- Methodical; as Darwin puts it:

One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. [...] The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds. (Darwin 1859, pp. 29–30)

In this case the presupposed factual statement would be:

Organisms with traits that perform a certain function in a more effective way *tend to be consciously selected for breeding by humans*, tending consequently

⁷ Gayon (1998, pp. 54–59); Wilner (2006); Álvarez (2010); Brandon (1978, 1990, p. 13), among others, also defend this point.

to improve, if the trait is inheritable, the success of those organisms in differential reproduction.⁸

- Unconscious; as Darwin puts it:

If there exist savages so barbarous as never to think of the inherited character of the offspring of their domestic animals, yet any one animal particularly useful to them, for any special purpose, would be carefully preserved during famines and other accidents, to which savages are so liable, and such choice animals would thus generally leave more offspring than the inferior ones; so that in this case there would be a kind of unconscious selection going on (Darwin 1859, p. 36).

In this case the presupposed factual statement would be:

Organisms with traits that perform a certain function in a more effective way *tend to be specially protected by humans*, tending consequently to improve, if the trait is inheritable, the success of those organisms in differential reproduction.

4.4.4 Group selection

The cases presented above have something in common: that natural selection is applied at an individual level. The trait that best performs the function, as well as fitness and reproductive success, all concern one and the same kind of individual organism. In some cases, though, individual natural selection does not seem to work. This happens, for instance, in the case of neutral insects. In the case of social insects, such as bees or ants, there can be castes of workers that have peculiar functional traits—that is, functional traits that are not shared by other castes—and, given the fact that such are sterile castes, it cannot be held that the possession of those traits by ancestors that are also sterile improved their differential reproduction. The way in which Darwin solved this problem involves the application of natural selection at levels above that of the individual.

⁸ One interesting issue with these sort of applications, which can also generate reasonable doubts about the attempt to reduce artificial selection to natural selection, is that in this case it may seem strange that the long tail of a dove produced by artificial selection has the function of improving the chances of crossings being attractive to the breeder. Nevertheless, it should be noted that in this sense the application does not seem different from the one in which a flower improves its chances of being crossed by being attractive to an insect. Nor is it different from the one that considers that a peacock improves its chances of crossing by looking attractive to females of their species. The issue deserves further discussion. Here I present these applications separately to adjust more to Darwin's writing, which usually presents artificial and natural selection as separate mechanisms, and considers that the case of insect attraction through flowers is not a case of sexual selection. Some authors, however, have found closer relations between artificial and sexual selection—e.g., Ghiselin considers the possibility that sexual selection is a variant of artificial selection (Ghiselin 1969, p. 246), which goes in the same direction as some statements by Darwin himself (1871, v.I, 259).

[...] under certain circumstances individual differences in the curvature or length of the proboscis, &c., too slight to be appreciated by us, might profit a bee or other insect, so that certain individuals would be able to obtain their food more quickly than others; and thus the communities to which they belonged would flourish and throw off many swarms inheriting the same peculiarities. (Darwin 1872, pp. 74–75)

The factual statement presupposed is:

Worker (sterile) bees with a curvature or length of the proboscis more effective for extracting nectar from certain flowers *improve the performance of the community they belong to*, tending consequently to improve, if the trait is inheritable, the reproductive success of that community.⁹

4.4.5 Other applications of the fundamental law of NNST

The aforementioned are not the only candidates for special laws of NNST. The theory's richness consists precisely in the possibility of accounting for new facts by finding new specifications of the concept of fitness. We can find a different application in an early text of Darwin:

[...] 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 1844, p. 92).

In this case the specialization of the fundamental law would be:

Organisms whose seeds have traits that enable them to glide in the wind tend to *disseminate those seeds better*, consequently tending to improve, if the trait is inheritable, the success of those organisms in differential reproduction.

This shows that in his first essays on the subject Darwin already conceived of a wide concept of natural selection that included applications that did not require an improvement in survival.

4.5 The fundamental law of NNST

From the observed cases we can obtain a general statement:

⁹ Regarding the reconstruction of NST, group selection as it was considered by Darwin is especially interesting, since entities of different level are interrelated in the same application. Below, I include "performance of the community they belong to" as a specification of fitness, but the complete formal reconstruction requires a better way of dealing with group selection cases (see Ginnobili 2012b).

Organisms that possess a trait that performs a function more effectively tend to improve ϕ , tending to improve, in consequence, if the trait is heritable, their own differential reproductive success or that of the community they belong to.

ϕ is the concept that assumes different specifications in the multiple specializations of the fundamental law: capacity to mate, survival, chance to cross, ability to spread seeds, utility to humans, performance of the community they belong to, etc.

Darwin never proposed a term for this concept—that is specified in different ways—because he never presented the fundamental law that unifies all specializations in a general way. The main thesis of my paper is that this general and abstract concept, implicit in the work of Darwin, is the “ecological fitness” I have been referring to in previous sections. The fact that Darwin neither makes the fundamental law of NNST explicit, nor names explicitly the most important concept of NNST, is not that surprising.¹⁰ Metatheoretical structuralists have found this to be quite common in theories that do not express their laws through a general equation, since they are not quantitative (e.g., Abreu 2012; Balzer and Göttner 1983; Balzer and Marcou 1989; Barutta and Lorenzano 2012; Blanco 2012; Gonzalo and Balzer 2012; Lorenzano 2002; Lorenzano et al. 2007; Peris-Viñe 2011).

If we call the concept ϕ “fitness” and we call the organisms that possess such traits “adequate” the main components of the fundamental law become explicit:

More adequate organisms tend to improve their fitness, tending to improve, in consequence, if the trait is heritable, their differential reproductive success.

These are the main components of the fundamental law of NNST. I do not claim these are all of its components. Nor that this is its exact shape—in this formulation I leave indeterminate, for instance, whether it is a probabilistic principle. It is just a sketch. But as we will see in the following sections, if these first steps of a reconstruction are accepted, important philosophical or metatheoretical consequences can be drawn and some light can be shed on several contemporary discussions about the theory of natural selection.

To provide some insight about the structure of this law—given that conditionals within conditionals are hard to express in natural language—I will present it semi-formally:

[(The trait r^1 is more effective than trait r^2 in performing function f in environment $e \rightarrow$ organisms that possess r^1 are fitter than those who possess r^2 in e) and traits r are heritable] \rightarrow the organisms that possess r^1 will be more successful in differential reproduction than those that possess r^2 in e .¹¹

¹⁰ An interesting precedent for the kind of work that tries to propose terms for concepts that function implicitly in practice, and which the title of this work is based on, is the article on the exaptations of Gould and Vrba (1982).

¹¹ The application of this principle is always *ceteris paribus* given the existence of other evolutionary mechanisms. A problem of this formulation arises in the vacuous satisfaction of the conditional. If the adequation of the trait does not produce an increment in the fitness, then the law will be true. An option is to replace the first conditional with a conjunction. But then the idea that the adequation that is relevant to

Where r is a kind of trait—e.g., the length of the neck of giraffes—and r^1 and r^2 are two different kinds of lengths of the neck—e.g., r^1 is a 1,10 m long neck and r^2 is a 1 m long neck—, f is a particular function—e.g., reaching the higher branches of trees—and e is a particular environment—e.g., the African savannah in a period of scarceness.¹² Another reason why this version is only a sketch of the fundamental law is that it is not broad enough, since it does not take into account (1) cases where more than two versions of the same trait are present, (2) cases where more than two kinds of traits are involved, and (3) cases that have trade-offs between different specifications of fitness. Of course, a wider account that overcomes those limitations would be valuable, but given the goals of this work—which focuses on the nature of the concept of ecological fitness and its applicability—it is not necessary to deal with these complications.¹³

Why is it necessary to resort to fitness? Why not think that the fundamental law only relates the effectiveness in the performance of a certain function with reproductive success? The answer to these questions is important because most of NNST reconstructions only take into account two components, whereas it is characteristic of this reconstruction to distinguish between the immediate function of the trait and *fitness*—which we may call an “evolutionary” or “mediate” function. The answer connects with the analysis shown before. Darwin always presents this threefold structure where (i) a non-evolutionary function—e.g., feeding from the nectar of certain flowers—is related to (ii) fitness, that is an evolutionary function—an improvement in survival due to better nutrition—, producing (iii) a greater success in differential reproduction. As I have claimed, if one of these elements is removed, either the function or fitness, explanations would become incomplete: the possession of a trait and reproductive success would cease to be related “causally” and explanations would no longer rise above the status of mere statistical correlations between the possession of the trait and reproductive success. The conditional in the antecedent of the law states that the function of a trait has evolutionary significance only if it implies an improvement in fitness.

Of course, the fact that there are usually only two elements considered in NST’s fundamental law may cause many readers to think of fitness and adequation as non-separate components; on the other hand, it may cause many others to conflate fitness with reproductive success. In fact, this tendency may vary in different applications of the theory. For example, sometimes it is possible to improve reproductive success by increasing fecundity—a case also considered by Darwin. In this case, fitness as fecundity may be confused with reproductive success. On the other hand, the function of attracting partners may be confused with fitness as mate capacity. Even

Footnote 11 continued

evolution produces an increment in the fitness is missed. Another option is to replace the material conditional with another kind of counterfactual conditional.

¹² Elsewhere I have reconstructed NNST formally in structuralist terms making explicit all the concepts necessary to account for this structure in a more meticulous way (Ginnobili 2012a). For reasons of space I only provide the informal version, which is sufficient for the purposes of this paper. There is another structuralist formal reconstruction of NNST in Mario Casanueva (2011).

¹³ Moreover, these are usual simplifications presupposed in the discussions of the fundamental law of NST. For example, Brandon (1980) or Kitcher (1993).

though this paper tries to focus on the explication of the concept of fitness, it is important to deal with the other concepts present in the law at least to be able to distinguish them from fitness.

The claim that functional concepts are constitutive of NNST may seem controversial and needs to be examined more thoroughly. In order to have a complete account, it would also be necessary to indicate the nature of functional explanations and functional concepts. I have dealt with these issues elsewhere (Ginnobili 2011a). I have maintained that the best way to explicate the functional language of NNST is by resorting to an underlying theory from which functional concepts come. I have tried to reconstruct this theory based on some texts by Darwin on crossed fertilization. In any case, the reconstruction of NNST that I present is compatible with minimalist interpretations of functional language—such as that put forward by Robert Cummins (1975). Given that these functional concepts are part of NNST, you cannot appeal to natural selection in order to define them in the way that, for example, the etiological approach does (Wright 1976; Millikan 1989; Ginnobili 2009; Caponi 2013). The distinction between fitness and function is based on the idea that many have that functional biology can be developed independently from evolutionary biology. Even though this idea may be metaphysically awkward to many authors I think that it better reflects both current and Darwinian biological practice, since both of them ascribe functions to traits independently of evolutionary considerations.¹⁴ This is an arguable matter, and although it is relevant for discussing the adequacy of the general reconstruction, it exceeds the limits of this paper.

Regarding the confusion between *fitness* and *reproductive success* mentioned above, it is worth noting that reproductive success should not be identified with fecundity. That is because reproductive success cannot be measured simply by counting offspring, as, in many cases, reproductive success can be increased by limiting the number of progeny. That is, the number of descendants an organism has could itself be an adaptive trait (Darwin 1859, p. 66). Counting the quantity of organisms of the same kind—with the same specific trait—in the next generation is one possibility. But this can only be done with heritable traits. If the trait is not heritable then the number of organisms that possesses the trait will not change in the next generation. That is the reason why heritability is introduced in the fundamental law.

Dealing with the explication of functional language and reproductive success in NST is complex and deserves more thorough treatment. For my purposes here it is enough to show in which sense they must be differentiated from fitness.¹⁵

¹⁴ The relation between functional biology and evolutionary biology in Darwin's texts is extremely interesting; nevertheless, treating it properly is not possible here. I have discussed this issue somewhere else (Ginnobili 2014).

¹⁵ The claim that the NNST's fundamental law includes at least these three concepts does not imply that every application includes only three elements. It is possible to have applications in which more traits interact, with more functions, with diverse specification of fitness. Special laws do not have to preserve the form of the fundamental law, even though they do have to maintain the same concepts and preserve certain essential relations among them.

4.6 NNST theory-net

In classical philosophy of science there is no other term used more equivocally than ‘theory’. The sense more generally intended, the one expressed when we speak of the ‘theory of Classical Particle Mechanics’, for instance, is that of ‘theory-net’, presented in Sect. 1. Often the fear of formulating a wider theory of natural selection—one that includes, for instance, sexual selection—is explained by the risk of creating a confusion between different mechanisms—as non-sexual natural selection and sexual selection—but this would be the result of employing a metatheoretical language that is not conceptually rich enough—for instance, with one single term for objects that are as distinct as theory-elements and theory-nets are. Since I am not offering an exhaustive reconstruction of NNST, but rather indicate the essential components of its fundamental law only, I will treat the theory-net as a ramification of laws. I will speak of the fundamental law rather than of the basic theory-element, and of special laws, rather than of specialized theory-elements.

Following the same intuition proposed by Endler on this topic (Endler 1986, p. 9; 1992)—though he does not use structuralist tools—I believe that the theory-net of NNST two great branches of specialization has in its application to individuals: the special law of sexual selection and the special law of non-sexual selection, or of natural selection in a narrower sense. The reason for this is that Darwin sometimes uses “natural selection” in the widest possible sense and other times in the more narrow sense, for instance, when he wants to confront it with sexual selection. I provide in Fig. 1 one of the possible expositions of the theory-net of NNST in which all the cases reviewed are accommodated.¹⁶

Regarding the way in which ecological fitness is applied it is important to remark that NST does not consist solely of one principle, but, as it is the case with Classical Particle Mechanics, it is a theory-net that regulates the different forms in which the principle can be applied and the different ways in which fundamental concepts can be specified. In order to apply NNST it is necessary to choose which kind of selective pressure is at stake, that is, to determine which special law is operating, or to create a new special law by finding a new way to specify the concept of fitness. In the same sense in which someone who works within Classical Particle Mechanics can study particle movements through an existing special law or create a new special law suggesting a new kind of force (that is always more controversial).

¹⁶ This theory-net arises only from the examined cases, that do not exhaust all the applications Darwin makes of NNST in the *Origin*, nor all the specializations used by Darwin in other texts or discovered by other biologists. These might change the structure in question. I think, for instance, that it is possible to include as specialization the principle of divergence, but this discussion would take up too much space. I do not expand the branch of group selection, because all the cases treated in this work imply an improvement in the survival of the group, but maybe it is possible to find the same subclasses that we find in the branch of individual selection. The theory-net presented, therefore, is neither complete nor the only way to present the available information, but rather a possible way to organize the cases we have been studying, which allows us to show the complex and unifying structure of NNST.

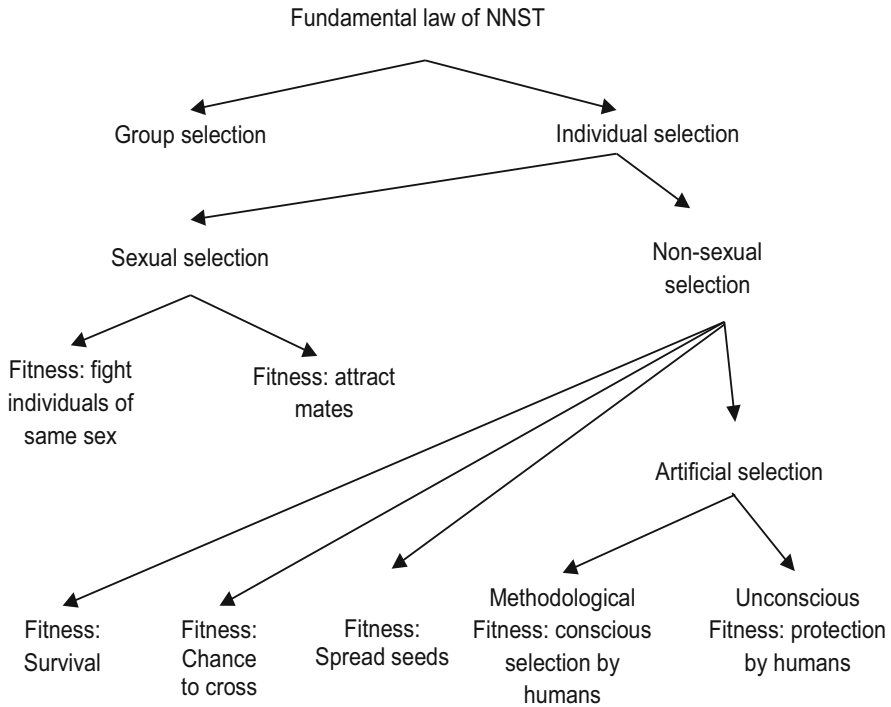


Fig. 1 Theory-net of NNST that arises from the different instantiations of fitness in the examined cases

5 Darwinian fitness, ecological fitness and population genetics fitness

The adequacy of the explication of a concept, or of the reconstruction of a theory, is to be judged by its clarity and its success in accounting for its object, but also, by its fruitfulness (Carnap 1950, pp. 3–15). One way to measure the fruitfulness of a reconstruction or of an explication is to consider the philosophical problems that it allows to solve. In this section I will try to show how fruitful the proposed reconstruction of Darwinian theory is. But before, I will show how this reconstruction can shed light on current uses of NST—at least in some relevant aspects.

5.1 Darwinian and current NNST

Even though a reconstruction of Darwinian NNST is already a result in its own right, I have presented such reconstruction because I think it also clarifies certain aspects of ecological fitness and the intuition some authors have that population genetics fitness is not sufficiently explanatory. This assumes that the informal reconstruction offered clarifies the contemporary NNST. My idea is that even if NNST might have suffered some essential change with respect to the Darwinian theory—e.g., in its intertheoretical links with genetic theories that were not

available in Darwin's time—the fundamental concepts pointed out are fundamentally the same, and, in particular, the threefold structure of its fundamental law—adequation, fitness and reproductive success—has not changed substantially. I want to emphasize two points as reasons to uphold this thesis. First, regarding the fact that an adequate reconstruction should make more concepts explicit, it should be said that the difference between the presentation of NST and its exemplifications in biology textbooks is evident. After a presentation that usually appeals solely to the satisfaction of three conditions: variation, inheritance, and differences in reproductive success—that can be considered at best as necessary conditions (Brandon 1990, pp. 6–9)—the functioning of natural selection is exemplified by cases in which every component pointed out in my reconstruction can be found. Using *Biston betularia* as an exemplar, for example, adequation as camouflage is distinguished from fitness as survival: moths that are better camouflaged tend to improve their survival (e.g., Dobzhansky et al. 1977, pp. 122–123; Ridley 1996, pp. 72–73). Using the evolution of the AIDS virus in an organism as an exemplar, on the other hand, the adequation as HIV resistance to 3TC is distinguished from fitness as fecundity: the strains of virus resistant to 3TC tend to improve their fertility; notice that in this case there are no changes in survival since the drug affects HIV's ability to reproduce without destroying it, showing that survival is not always involved in every application of NNTS (Ridley 2004, pp. 74–75). Second, regarding the branched structure of NNST, my point is that the different specifications of the fitness concept can be found in contemporary evolutionary biology literature: survival (Conner and Corcoran 2012), fecundity (Crone 2001), ability to disseminate seeds (Levin et al. 2003), ability to attract mates (Ryan and Cummings 2013), and the ability to fight individuals of the same sex for mating (Emlen 2008), etc.¹⁷

5.2 NNST and population genetics

This view of natural selection implies taking distance from the authors—see Sect. 1—that believe that population genetics provides a quantified version of NNST. It also strengthens the point of those who consider—see also Sect. 1—that

¹⁷ Tim Lewens (2007, pp. 58–62) thinks that contemporary NST differs from Darwinian NST, since in contemporary NST the struggle for existence is not essential, as it is in Darwinian NST. In my reconstruction of Darwinian NST the struggle for existence—in Darwinian terms, the fact that more individuals are born than those that can survive—does not appear. This may seem a problem, but I think I have given enough bibliographic support to the idea that the struggle for existence understood as a struggle for survival is not always involved. If we think of the struggle for existence in a broad and metaphorical sense—as Darwin asks us to do (1859, p. 62)—as a struggle for leaving progeny, then there would be no difference between contemporary NST and Darwinian Theory. This metaphorical sense is covered by my reconstruction. Maybe the point raised by Lewens has to do with the role of limitations of resources that appear in the abstract way in which Darwin usually presents natural selection—as an inference from the geometric growth of populations, the arithmetic growth of food, the variation and the tendency to inherit variations, among other things (Darwin 1859, pp. 80–81). There are two points to be made about this. First, there is no reason to think that natural selection can only work in cases of limited resources (Barbadilla 1990, p. 172; Sober 1993, p. 194). Second, Darwin himself did not think that the cited argument results the theory of natural selection, but is an argument that makes natural selection probable (Darwin 1883, v. I p. 9; Gayon 1998, p. 23). This argument, moreover, should not be confused with the structure of the theory (Kitcher 1993, pp. 34–37).

population genetics resorts to NNST to explain why certain organisms have greater reproductive success—“selective pressures” are often spoken of in this sense.

The following analogy can be useful to discuss the issue. Just as in a Newtonian world it may be inferred from the acceleration of a particle that a force (or an interaction of forces) has acted, in much the same way, in a world in which migration, genetic drift, mutation, selective mating and natural selection are the only forces assumed to act on the genetic frequencies of a population it may be inferred from the genetic frequency of a population not being as expected, and the confirmation that no other factors considered by population genetics has had an influence, that natural selection has acted and its action can be measured (assuming the Hardy–Weinberg law). But pointing out that there are reasons to believe that natural selection has acted is not equivalent to applying NNST, much in the same way that in the supposed Newtonian world pointing out that a force or a combination of forces is responsible for the change in acceleration is not equivalent to applying Classical Particle Mechanics. An application of Classical Particle Mechanics implies determining the number and nature of the forces in action. Likewise, applying NNST implies finding the trait that is being used more effectively and the connection between that trait and reproductive success, what I have called ‘fitness’. Just as in the Newtonian example there can be a combination of forces of different nature acting on a particle, the same can happen in the application of NNST. Selective pressure might be generated by a combination of, for instance, survival and the ability to attract mates (Frost 1994; Darwin 1871, pp. 278–279; Allen et al. 2011); or by the compromise between two survival pressures, as in the case of bipedalism and brain size in the process of hominization (Rosenberg 1992; Leutenegger 1987). To conclude, the mere determination of the existence and strength of a selective pressure is not equivalent to applying NNST. The more complete version of NNST I offer shows this more clearly. In addition, it allows us to see that ecological fitness explains the differences in reproductive rates that population genetics can determine clearly (in certain populations). In this sense, it can be held that ecological fitness explains population genetics fitness (Rosenberg 1994, pp. 110–111) and NNST cannot be explicated by reconstructing population genetics.

5.3 Incompleteness of available NNST reconstructions

Regarding NNST reconstructions that consider NST as independent from population genetics (Williams 1970; Rosenberg 1983; Tuomi et al. 1988; Tuomi and Haukioja 1979; Brandon 1990, 1980, 1978; Endler 1986) it should be noticed that they fail to give an account of all the concepts involved in selectionist explanations (since they do not distinguish between *adequation* and *fitness*), but also do not reflect properly the way in which the fitness concept is applied through the specifications displayed in the net-theory of NNST (see above Sect. 4).

If I am right, then the available reconstructions of HNST and NNST are incomplete in this sense. Due to space limitations I can’t review every available reconstruction. I will only treat Brandon’s view of natural selection as exemplar, given its influence, clarity, and closeness to my proposal—both in its dealing with

NNST instead of HNST, and in its treatment of NNST through his fundamental law. The fundamental law of NNST according to Brandon (1990) is:

If a is better adapted than b to an environment e , then (probably) a will have a greater reproductive success than b in e .

Brandon seeks a law that through proper specifications might lead to specific properties in such a way that from his version of the law we might obtain, for instance by quoting the famous case of *Biston betularia*, statements like: “If a is darker winged than b (in E) then (probably) a will have more offspring than b (in E)” (Brandon 1980; 1990, p. 23). The way in which the statement is obtained is by replacing the propensity to leave more descendants with one of its physical realizations, in this case, the colour of the wings. The reconstruction of the famous case of *Biston betularia* quoted by Brandon, which constitutes a paradigmatic example of directional NNST, is, however, incomplete. This is an interesting case because it shows that all the concepts I claim to be constitutive of the theory appear not only in Darwin’s applications of NNST, but also, as pointed out above, in more contemporary versions (Dobzhansky et al. 1977, pp. 122–123; Ridley 1996, pp. 72–73).

The complete explanation would have the following components:

Moths of darker coloured wings are better camouflaged in their environment to the eyes of predators, thus tending to improve their survival and, tending consequently to improve, the trait being inheritable, their success in differential reproduction.

This explanation has all the components featured by my reconstruction. Brandon mentions them when he narrates the case (Brandon 1990, pp. 22–23) but his law does not give account of them, since the function—i.e., camouflage—is missing. It is interesting to emphasize that in Henry Kettlewell’s original works (1956, 1955) it was essential not only to find a correlation between differential reproductive success and the colour of the wings, but also, and that is what many of his experiments were about, to determine that this correlation is accounted for by the ability to camouflage from natural predators.

5.4 Heterogeneity of the concept of ecological fitness

Besides its incompleteness, Brandon’s presentation of NNST also allows me to point out something else about the application of the theory. Notice that the *Biston betularia* case is a direct instantiation of the fundamental law and compare this direct application with the application through special laws in my view of NNST. The reconstruction of the theory-net of NNST allows us to deal with the problem exposed in Sect. 3 in a more adequate way. The question of how ecological fitness is related to the particular properties of organisms can be resolved from the reconstruction of the theory itself, without a need to resort to any peculiar metatheoretical (or even metaphysical) concept as supervenience, and without turning the NNST fundamental law into a part of the theory of probability, as seems to be the case in the propensity interpretation of fitness.

We want to reconstruct or explicate adequately the kind of explanation given by Darwin or by Kettlewell, where it is not enough to find a correlation between certain kinds of organisms and their ability to leave descendants, but where there is an appeal to certain other features of organisms that are different from their reproductive success. I think my reconstruction accounts better for these intuitions regarding the concept of fitness, making use of the tools that metatheoretical structuralism provides. The point is that it is not necessary to resort to a particular ability of organisms for fitness that is supposed to be different from their differential reproductive success. If by “the ability of organisms” we mean, for instance, the fact that an increment in fitness can be due to the development of an ability to fly to escape from predators (Rosenberg 1978, p. 371), in my reconstruction of NNST this does not have to do with specifications of fitness, but rather with specifications of the part of the law that concerns adequation—the function of the trait. Brandon says that the reason why fitness cannot be identified with any particular property or ability of organisms is that the increment in fitness may be due to different causes, e.g., to an improvement in fecundity or survival, as Brandon holds (Brandon 1990, p. 13). The proper answer to this issue consists—resorting to the notions of metatheoretical structuralism—in pointing out that, in effect, fitness is not identical to, nor even implied by, any of these abilities, but is indeed specified in these different abilities in the different special laws of NNST.

This response was not available either for Rosenberg or Brandon, since they lack a metatheory that accounts for the way in which the fundamental law of a theory is specialized in the special laws that arise from the specifications of its fundamental concepts until terminal specializations, where nothing remains to be specified, are reached. In each case, applications of the theory arise directly from the fundamental law by direct instantiations of its concepts. So, if the concept of fitness were directly instantiated, it would seem that its applications are extremely heterogeneous. But as I have already shown, this is not the case: the concept of fitness is specified in different ways through many implicit special laws that regiment its acceptable uses. The fact that the set of relevant properties is heterogeneous and devoid of defined boundaries entails no metatheoretical problem in the reconstruction of the theory. Imagine how overwhelmingly heterogeneous the concept of force would seem if we did not consider the special laws of Classical Particle Mechanics.

Moreover, to have abstract concepts that are specified in heterogeneous ways—as it happens with *force* in Classical Particle Mechanics—is a characteristic feature of unifying theories (Moulines 1982). The openness of such concepts is related to this unifying force since it is possible to discover new special laws through the discovery of new ways of specifying those concepts. Of course, *which* are possible specifications of such concepts is an empirical question that is to be determined by the development of the theory.¹⁸

¹⁸ There are two ways in which we can say that Darwinian theories have unifying power, both present in Darwin’s texts. The first one has to do with the fact that Darwinian evolutionary biology can unify data from different disciplines (geology, embryology, systematic, biogeography, etc.; see e.g., Ruse 1998, p. 3). The second one has to do with the fact that NNST has a wide and heterogeneous set of intended applications, in the same sense that Classical Particle Mechanics has (for example, Kitcher 1981, 1993). This latter sense is the one alluded to in this work.

Let me put this in other words. Sober thinks of evolutionary biology as a theory of forces. The theory of forces must contain, according to Sober, both source laws—which describe the circumstances that produce forces—and consequence laws—which describe how forces, once they exist, produce changes in the systems they impinge upon.

The physical circumstances that can generate fitness differences are many. Perhaps someday these will be regimented and reduced in number. But at present evolutionary theory offers a multiplicity of models suggesting a thousand avenues whereby the morphology, physiology, and behaviour of organisms can be related to the environment in such a way that a selection process is set in motion.

The supervenience of fitness – the fact that fitness is not a single physical property – helps explain why general source laws are hard to come by in evolutionary theory. (Sober 1993, p. 51)

Having in mind the terminology of Sober, the reconstruction of the theory-net of NNST displays the implicit set of source laws showing that in this respect NNST is not different from Classical Particle Mechanics. Both the relation of specialization and the notion of theory-net provided by metatheoretical structuralism contribute to showing this implicit net and permit explication of the way that NNST works, more accurately than the notion of supervenience.

5.5 Metatheoretical nature of NNST

The most important advantage of the way we have dealt with NNST is that, under this view, the theory does not have a peculiar status. A lot has been said about possible analogies between classical particle mechanics and evolutionary biology (Williams 1980; Sober 1993; McShea and Brandon 2010; Brandon 2006; Stephens 2004). Appealing to metatheoretical structuralism allows me to show an overlooked sense in which NNST resembles Classical Particle Mechanics. According to Brandon, the fundamental principle of NNST is an instantiation of what he calls “the Principle of Direct Inference in Probability Theory” (Brandon 2006, p. 333, 1978) which is a principle that permits to infer actual frequencies from statistical probabilities. This is intrinsically related to Brandon’s appeal to a propensity interpretation of probability in order to explicate fitness. To consider NNST’s fundamental law as an instantiation of Probability Theory and to account for the ways in which the concept of fitness acquires empirical content by appealing to the physical propensity of organisms to leave descendants, would imply that NNST has a peculiar status as a scientific theory—McShea and Brandon (2010, pp. 108–109) think, for example, that probability theory is the reductive foundation for all evolutionary biology. This could be a high price to pay in the face of the existing detractors of NNST. From my perspective fitness is a very abstract factual concept, which acquires empirical content through its specification in the special laws of NNST. In this sense, the theory-net of NNST regulates the different kinds of acceptable specifications of fitness in the same way that Classical Particle

Mechanics regulates the acceptable different specifications of the concept of force. Metatheoretical structuralism shows that NNST does not differ from other biological theories, or even from theories in other disciplines, regarding the way in which its concepts acquire empirical content (Díez and Lorenzano 2013). Its notions of *theory-net* and *specialization* seem to be more adequate, in this sense, to deal with the matter of the nature of ecological fitness and the nature of NNST than the notion of *fitness as propensity*. Brandon's thesis that the natural selection principle is a schematic non-testable law—at least not on its own—is essentially correct (Brandon 1980). But once again, this feature arises not because evolutionary biology is nothing more than probability theory, but—as it was shown by metatheoretical structuralism—because factual fundamental laws of unifying theories often have this feature.

Let me go back to the concept of supervenience but leaving aside the metaphysical matter, and considering the word “supervenience” as expressing a metatheoretical concept that explains the way in which certain scientific concepts relate with each other in scientific practice. If by any chance anyone still thinks it as an interesting way to deal with these issues, it should be said that fitness “supervenes” on physical capacities of organisms *in the same way* in which forces “supervene” on physical dispositions of particles. In other words, it should be clear that NNST has no peculiar status and that those alleged peculiarities—often perceived as flaws—which lead some authors to appeal to the concept of supervenience in the first place, are usually constitutive characteristics of unifying theories, and in this sense, constitutive of the explanatory force of Darwin's theory.

6 Conclusions

In this work I have presented an informal reconstruction of the Darwinian NNST. On the one hand, such reconstruction helps clarify Darwin's thinking by presenting his theory more completely and showing its unifying power, something he considered to be the strongest argument for it, since NNST—as Classical Particle Mechanics—can be seen as a theory-net with various special laws that allow us to deal with an heterogeneous set of phenomena. Moreover, I tried to show the value of this reconstruction for certain debates that exist in contemporary philosophy of biology, especially those that deal with the role of NNST in evolutionary biology, with the nature of NST, and with the nature of its main concept: ecological fitness. In particular, I have tried to show that it is possible to give an account of the heterogeneity of applications of the concept of ecological fitness, by appealing to metatheoretical structuralism. This last point has allowed me to show that NNST is not a theory of a peculiar nature. The concept of fitness operates in a metatheoretical way analogous to other concepts in paradigmatic theories such as Classical Particle Mechanics. To demonstrate this last point, it was necessary to present a more complete version of NNST, making explicit concepts that are not considered in usual reconstructions. The explanatory component of the theory—the “causes” of differences in reproductive success—must be split into two different concepts: adaptation and (ecological) fitness.

Darwin's thought has played a central role in the constitution of contemporary scientific and philosophical thought. Also, in Darwin's thought a central role is played by NST, the theory that provided an account of the adequation of organisms to the environments they live in. The proper reconstruction of this theory, one that preserves its scientific and philosophical importance, constitutes the purpose of this work. If I am correct, none of the available reconstructions have taken into consideration all the concepts involved in the use of NST.

Acknowledgments I would like to thank Martín Ahualli, Daniel Blanco, José Díez, Pablo Lorenzano, Andrea Melamed, Luciano Piazza and Ariel Roffé for their helpful comments on previous versions of this paper. Also, I am especially grateful to Staffan Mueller-Wille for his careful work as an editor with this paper. This research was supported by the research projects PICT-2014-1741, PICT-2012-2662 (ANPCyT, Argentina), PIP No. 112-201101-01135 (CONICET, Argentina) and 32/15 255 (UNTREF, Argentina).

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