Probabilistic causation and the explanatory role of natural selection

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ABSTRACT

The explanatory role of natural selection is one of the long-term debates in evolutionary biology. Nevertheless, the consensus has been slippery because conceptual confusions and the absence of a unified, formal causal model that integrates different explanatory scopes of natural selection. In this study we attempt to examine two questions: (i) What can the theory of natural selection explain? and (ii) Is there a causal or explanatory model that integrates all natural selection explananda? For the first question, we argue that five explananda have been assigned to the theory of natural selection and that four of them may be actually considered explananda of natural selection. For the second question, we claim that a probabilistic conception of causality and the statistical relevance concept of explanation are both good models for understanding the explanatory role of natural selection. We review the biological and philosophical disputes about the explanatory role of natural selection and formalize some explananda in probabilistic terms using classical results from population genetics. Most of these explananda have been discussed in philosophical terms but some of them have been mixed up and confused. We analyze and set the limits of these problems.

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1. Introduction

Since the very beginning of the development of the theory of natural selection there has been disagreement about what natural selection can and cannot explain. There is currently a consensus that natural selection can explain the trans-generational propagation and maintenance of traits in populations. Although these explananda are taken as being only one, we shall show that they are very different. In spite of this consensus, there is no agreement about natural selection being able to explain something else, although at least three other explananda have been proposed for natural selection.

The first and the oldest is the question about the origin of organismal traits. Natural selection is usually thought as differential reproductive success of individuals associated with their different individual traits, while the origin of these traits is usually attributed to genetic mutations. From this point of view, it is concluded that natural selection does not explain the origin of traits but rather they are pre-assumed by it. We shall call this position the 'Non-creative View'. This viewpoint represents the opinion of many biologists and philosophers from the 19th century to the present (see Table 1). Those who have endorsed this position argue that natural selection is a "destructive" force because it simply eliminates or fixes already existing traits, but it does not "create" new traits—this view proposes that the only creative force of evolution is mutation. According to Morgan (1932) natural selection merely preserves certain traits and simply, in the absence of natural selection, in addition to the known forms of life, a vast assemblage of other types would exist which have been destroyed by selection (Huxley, 1936, 1943). The opposed vision is as old as the Non-creative View (see Table 1). This vision asserts that natural selection is a creative force because it can generate new traits by the cumulative selection that makes probable a combination of mutations which are necessary for trait development and that would not probably be combined together without natural selection. We shall call this position the 'Creative View'. In this vein,

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Table 1
Publications that defend the 'Non-creative View' or the 'Creative View' about whether natural selection can explain the origin of traits. Question marks mean that we are not sure of the work's category ascribed.

Non-creative Views of natural selection	Creative Views of natural selection
Lyell (1860)	Darwin (1859)
Mivart (1871)	Weismann (1896)
Cope (1887)	Muller (1929)
Eimer (1890)	Fisher (1932)
De Vries (1904)?	Fisher (1934)
Morgan (1905)	Huxley (1936)
Osborn (1909)	Huxley (1943)
Punnet (1911)	Simpson (1944)
Hogben (1930)	Simpson (1947)
Morgan (1932)	Muller (1949)
Uexküll (1945)	Simpson (1951)
Berg (1969)	Fisher (1954)
Grene (1974)	Dobzhansky (1954)
Cummins (1975)?	Lerner (1959)
Nagel (1977)?	Kimura (1961)
Wassermann (1981)	Mayr (1963)
Maturana and Varela (1984)	Ayala (1970)
Endler (1986)	Dobzhansky (1974)
Brooks and O'Grady (1986)	Gould (1977)
Dretske (1988)?	Gould (1982)
Saunders (1989)	Dawkins (1986)
Dretske (1990)?	Neander (1988)
Maturana and Mpodozis (1992)	Gould (1988)
Fontana and Buss (1994)	Maynard-Smith (1989)
Gilbert et al. (1996)	Millikan (1990)
Arthur (1997)	Godfrey-Smith (1992)
Mahner and Bunge (1997)	Ayala (1994)
Horst (1999)	Doolittle (1994)
Maturana and Mpodozis (2000)	Neander (1995a,b)
Arthur (2000)	Gould (1995)
Walsh (2000)	Dawkins (1996)
Macpherson (2002)	Walsh (1998)
Muller (2003)	Ayala (2000)
Muller and Newman (2003)	Gould (2002)
Ariew (2003)	Nanay (2005)
Lickliter (2003)	Forber (2005)
Reid (2007)	Ayala (2007)
Badyaev (2008)	Avise and Ayala (2007)
Lickliter (2008)	

Table 2
Publications that defend the 'Negative View' or the 'Positive View' about whether natural selection can explain why identified individuals have the traits they do (the trait identity). Question marks mean that we are not sure of the work's category ascribed.

Negative Views of NS	Positive Views of NS
Nozick (1974)	Neander (1988, 1995a,b)
Sober (1984)	Matthen (1999)
Sober (1995)	Nanay (2002)?
Walsh (1998)	Matthen (2002)
Pust (2001)	Matthen (2003)
Lewens (2001)	Nanay (2005)
Pust (2004)	Forber (2005)?
Stegmann (2010a, 2010b)	Nanay (2010)

Table 3
General textbooks of evolutionary biology and the number of pages explicitly dedicated to the mention, description or analysis of the creative effect of natural selection.

Textbook	Number of pages
Futuyma (1998)	0
Ridley (1999)	1
Maynard Smith (1989, 1998)	5
Fox et al. (2001)	0
Mayr (1963)	2
Freeman and Herron (2001)	0
Strickberger (2000)	2
Soler (ed.) (2002)	0

R. Fisher termed this process 'a mechanism for generating an exceedingly high degree of improbability' (Huxley, 1936),[1] and it was for the first time clearly pictured by Muller (1929) as the explanation of the origin of organismal features. Many scientists who took part in the development of the modern synthesis hold the Creative View (see Table 1), and several state that it constitutes the Darwin's greatest discovery and a major part of the essence of the Darwinian revolution (e.g., Avise & Ayala, 2007; Ayala, 1994, 2000, 2007; Dawkins, 1986; Gould, 1977, 1982, 1988, 2002). However, current evolutionary biology textbooks do not mention or allocate just a few pages to describe this process (Table 3), and moreover their description is often metaphoric or expressed in analogical terms. Furthermore, although this explanandum deals with a probabilistic argument, up to the present there is no probabilistic formalization of the creative effect of natural selection.

The fourth explanandum proposed for natural selection is very recent and we shall call it the 'trait identity'. The key question here is about natural selection being able to explain why a given existing individual (namely you, I, Peter or Robert), has the traits it does have. Those who defend the affirmative position (the 'Positive View', see Table 2) claim that the effect of natural selection on

lineages affects the identity of individual organisms. If the identity of each individual organism necessarily has the property of having been produced by the organisms which in fact produced it ('origin essentialism' thesis), then natural selection explains its identity, and thus its traits (Matthen, 1999, 2002, 2003). The other side of the debate (the 'Negative View', see Table 2), shares the argument that natural selection cannot explain why particular individuals have the traits they do because natural selection can only alter population properties but not individual properties. That is, natural selection cannot explain the properties of particular individuals. A byproduct of this debate has been the proposal that natural selection can explain why such and such an individual organism exists (although not why it has the traits it has). We shall call this fifth explanandum the 'individual existence'. As far as we know, nobody has opposed to this point, but certain arguments could be raised against it.

The relationships among these five explananda (maintenance of traits, propagation of traits, origin of traits, traits identity and individual existence) are by themselves a matter of dispute, and the position with respect to these relationships influences the position regarding the status of each explanandum.[2] Thus, Neander (1995b, p. 64), holds that a negative answer to the question on the origin of traits (she called it the 'Creation Question') entails a negative answer to the trait identity question, while others (Matthen, 1999, p. 149; Nanay, 2005, pp. 7–8; Neander, 1988, p. 426) hold that a positive answer to the propagation and maintenance of traits question entails a positive answer to the trait identity question. Nevertheless, these arguments do not persuade the partisans of the Negative View (Lewens, 2001, Pust, 2004, Sober, 1995, Walsh, 1998). In fact, Walsh (1998) denies that changes in frequency or creation (origin) of trait types influence individual traits.

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[1] For a review of different evolutionary ways to generate improbable states see Razeto-Barry & Cienfuegos (2011).

[2] We centered the discussion on traits and organismal selection but we believe that similar arguments can be made for other organismal units (alleles, genotypes, phenotypic modules) and maybe other units of selection (genes, species, clades).

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A systematic approach to these issues may be useful to resolve these disputes, or at least to put them on the same ground. Stephens (2007) claims that a resolution of this issue depends on which concept of explanation we assume. Nevertheless, it is not clear what concept of explanation leads to which conclusion, nor which concept is most appropriate for analyzing this problem. On the other hand, Huneman (2007) has emphasized the difficulty of natural selection explanations to fit a nomological model of explanation. In this study we shall show that the probabilistic approach to causality and explanation is a good common framework to confront these problems from a comprehensive point of view.

2. Probabilistic causation and statistical relevance

Probabilistic approaches to causation and explanation have a relatively long history. The core aspect of the theory maintains that causes raise the probability of their effects. Thus, the simplest version of the probabilistic theory of causation maintains that the factor A is a cause of B if and only if $P(B|A) > P(B|\neg A)$, where $P(B|A)$ represents the conditional probability of B, given A. This Probability-Rising theory has suffered strong criticism (see Hitchcock, 2002, for a review). In response to the critics, particularly to avoid the problem of spurious correlation, Reichenbach (1956, sec. 23) and Suppes (1970, Ch. 2) proposed a 'no screening off' condition, and the more recent Test Situations theory (TS) was proposed by Cartwright (1979) and Skyrms (1980), and generalized by Eells (1991, Ch. 2–4) and Hitchcock (1993). According to the TS theory of probabilistic causation, A causes B if and only if $P(B|A \,\&\, T) > P(B|\neg A \,\&\, T)$ for every test situation T, where a test situation is a conjunction of factors some of which are specifically required to remain fixed.

On the other hand, coming from the same tradition of probabilistic causation, Jeffrey (1969), Salmon (1971a, 1971b, 1984) and Greeno (1970) developed the Statistical Relevance (SR) model of scientific explanation. The essence of the SR model is that an attribute A is explanatorily relevant to an attribute B if $P(B|A) \neq P(B|\neg A)$. The SR model is similar to the TS theory of probabilistic causation, but implies the specification of a partition of the possible conditions related to the attribute and the information about their specific probabilities. We shall take the TS theory and SR model as a general causal and explanatory framework for the natural selection explananda. For our goals the statistical situations of the TS theory and the partition of the SR model are considered as controlled, *ceteris paribus*, and without factors screening off the probabilistic relations considered. This is the usual assumption in the population genetics and molecular evolutionary theories that will be the basis of our formalization (Crow & Kimura, 1970; Ewens, 2004). Thus, we can take the essential core of TS and SR as:

$$A \text{ causes } B \text{ if and only if } P(B|A \,\&\, T) > P(B|\neg A \,\&\, T) \tag{1}$$

$$A \text{ is explanatorily relevant to } B \text{ if and only if } P(B|A \,\&\, T) \neq P(B|\neg A \,\&\, T) \tag{2}$$

Thus, the explanatory relevance is guaranteed when probabilistic causation is proved. We shall attempt to show that all valid explanantia from the natural selection theory are understandable from the probabilistic approach to causation and explanation.[3] This attempt is facilitated because the population genetics theory is mainly developed in probabilistic terms (Crow & Kimura, 1970; Ewens, 2004).

3. Explaining the propagation and maintenance of traits

Since Darwin's and Wallace's (1858) and Darwin's (1859) foundational works, the only consensus about the explanatory role of natural selection is that it explains the propagation of new mutant traits (and lost of the wild-type) and the maintenance of the wild-type traits (and lost of the new mutants) in nature. Nevertheless, at the same time that they are the most accepted explananda of natural selection, they are rarely analyzed conceptually. For example, it has been commonplace to take the propagation of traits and the maintenance of traits, as equivalent or implied explananda (e.g., Neander, 1988, 1995a; Walsh, 1998). However, they constitute two very different and not implied explananda. The difference between selective propagation and selective maintenance comes from the difference between positive and negative (=purifying) selection (both generally indistinctly represented by the common metaphor of the sieve, e.g., Dawkins, 1986). Natural selection can explain the *propagation* of a trait (or trait variant) if individuals with a *new* heritable trait have higher fitness than their conspecifics (i.e., if the reproductive success of these individuals with the mutation is higher than the wild-type) and their frequency in the population increases.[4] On the other hand, natural selection can explain the *maintenance* of traits if individuals with any *new* heritable variation of the trait have lower fitness than their conspecifics and they do not persist in the population (Fig. 1). Recently, Valenzuela and Santos (1996) and Valenzuela (2000) have proposed the use of 'substitution' and 'fixation' as denoting different concepts in population genetics because a genetic substitution (a mutation propagated to all population or species) could not be maintained as "fixed" through time. Thus, a mutation propagated until substituting the wild-type (i.e., a 'substitution') does not necessarily is preserved in the population (i.e., it does not necessarily is a 'fixation').

It is clear that the selective explanation of the propagation and maintenance of a trait depends on the positive and purifying selection, respectively. If positive and purifying selection are distinguishable processes then the propagation and maintenance of traits are distinct explananda of natural selection. That positive and purifying selection are distinguishable processes can be based on four major arguments. First, the propagation by positive selection consists of a relatively long polymorphic transient phase between two times of different states of the population, while the maintenance by purifying selection has only a relatively very short polymorphic phase. Second, purifying selection cannot be cumulative while positive selection can, that is, purifying selection does not add variants for an accumulable series, while positive selection does it. Third, although positive selection favoring individuals with the advantaged new trait may seem equivalent to a process of purifying selection disfavoring the disadvantaged wild-type, these processes are not alike at all. Negative selection acts during a short time period meanwhile the new trait is transiently present in the population. By contrast positive selection acts for a longer time period until the new trait is substituted. In the beginning of the substitution by positive selection, the process seems similar to a purifying selection process: one or a few variants are successfully reproduced and the others are unsuccessfully reproduced (Fig. 2). Nevertheless, in the purifying process, disadvantageous mutations would have been arisen recently (Fig. 2b) while in positive selection, the (relatively) disadvantageous trait corresponds to the ancestral wild-type of the population (Fig. 2a). That is, to attain this state by negative selection N-1 mutations with low fitness would be necessary, and this

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[3] For other analyses of natural selection theory as a probabilistic theory see Hodge (1987, 2001) and Millstein (2002, 2006).

[4] We emphasize that natural selection 'can explain' instead of 'explain' (a common use in the literature), because it does not necessarily explain the propagation of the trait. For example, in small populations or for traits with very slight effect on fitness, the propagation of a trait with higher (or lower) fitness than the wild-type could be explained mainly by stochastic processes as genetic drift if |Ns| < 1, where s is the selection coefficient of the trait and N the population size (Crow & Kimura, 1970).

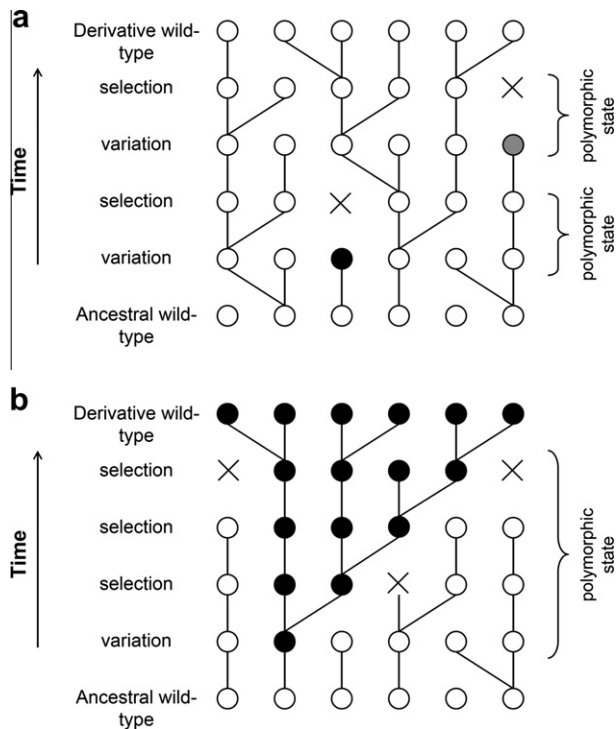ARTICLE IN PRESS

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Fig. 1. (a) Maintenance of a trait by permanent processes of negative (or purifying) selection. New variants (full circles) with lower fitness than wild-type (white circles) are eliminated in the short term because of their selective disadvantage. Individuals eliminated have recent new mutations. (b) Propagation of a trait by a process of positive selection. The new variant (black circle) with higher fitness than wild-type (white circles) is propagated because of its selective advantage. Individuals eliminated do not have the new mutation.

Fig. 2. (a) A very short process of positive selection: a one-generation substitution in t_2 of a new advantageous trait (black circle) arising in t_1 and the elimination of the N-1 ancestral individuals wild-type (white circles) of t_0. (b) A thought particular process of purifying selection: Substitution in t_2 of an ancestral advantageous variant (black circle) and the elimination of N-1 new disadvantageous traits (white circles) arising by mutation in t_1 from the wild-type ancestral individuals of t_0. The steps $t_1 \rightarrow t_2$ are identical both for (a) and (b), but in (b) we assume a multiple mutation event arising from traits with lower fitness than the wild-type, that is a biologically implausible event.

is biologically unrealistic. The real difference between positive and negative selection becomes clearer in the assertion that natural selection is a two-step process (Mayr, 1962, 1978, 1994, 1997).[5] Positive selection does not entail that there are no individuals eliminated (or without descendants), but it implies that more frequently individuals with the ancestral wild-type are eliminated than individuals with the recent mutation (or, in reproductive terms, that individuals with the recent mutation leave more offspring than those with the wild-type). Fourth, the result of a population under positive selection is a population with higher absolute fitness[6] (and possibly higher population size[7]), while the result of a population under purifying selection, *ceteris paribus* (particularly, without later environmental changes), is a population with the same absolute fitness (and the same population size). In other words, positive selection causes the change of species, while purifying selection the non-change (stasis) of species.

It is important to clarify that we should not confuse the positive/purifying selection differentiation with the problem of the positive/negative *target* of selection (Mayr, 1994, 1997). When a selective agent interacts with some but not all of the individuals of a population, we may ask whether the selective

interaction occurs with the fittest individuals or with the less fit individuals, i.e., whether the target of selection is the advantageous or the disadvantageous individual. By and large the target of selection is thought to consist of the individuals with lower fitness or the eliminated individuals (Mayr, 1994, 1997), e.g., in predation processes the selective agent (predator) interacts with the eliminated (prey), but also the targets can be subjects with higher fitness, e.g., the subjects chosen for mating in a sexual selection process. Positive and purifying selection are processes that can act both if the target of selection is the advantaged and if it is the disadvantaged individual. For example, in the case of purifying selection, individuals with a new disadvantageous trait might not be a target of selection because they are not (positive) target of mate choice or might be a target of selection because they are (negative) target of predation. Then, positive/purifying selection and positive/negative target of selection are two orthogonal distinctions.

The probabilistic causation of natural selection in the propagation of traits can be formalized for a simple process of positive selection (Fig. 3a). Natural selection (*NS*) explains that a recent rare mutation that generates a trait *T* spreads until it substitutes the wild-type if:

$$P(f_t(T) \approx 1 | NS \ \& \ f_{t_0}(T) = p) > P(f_t(T) \approx 1 | \neg NS \ \& \ f_{t_0}(T) = p) \qquad (3)$$

It is a classical population genetic result (Crow & Kimura, 1970) that if a trait *T* has a positive selection coefficient *s*, the probability of

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[5] "Darwinian selection, as it is now fully understood by the evolutionists, is a two-step process. The first step is the production of a vast amount of variation that will serve as the material needed for the second step, the actual process of selection or elimination." (Mayr, 1997, p. 2091). At long-term, the possible fates of a mutation are loss or fixation, which is commonly represented in population genetic models considering that frequencies 1 and 0 of a new allele are "absorbing barriers" (Crow & Kimura, 1970, p. 379). However, note that polymorphisms are possible to maintain in equilibrium frequency ($\neq 0$ and $\neq 1$) by significant time in sexual populations by heterosis or by changes of relative fitness in time.

[6] This assertion corresponds to The Fundamental Theorem of Natural Selection (Fisher, 1930; Frank & Slatkin, 1992), which is valid without frequency dependent selection (Sober, 2000).

[7] Note that the carrying capacity can be understood as a dynamic quantity (Sayre, 2008). The common assumption in mathematical population genetics is that the population size is constant during the process of mutations substitution. Nevertheless, the change of population size due to the substitution process has been recently incorporated in population genetics literature (Gabriel et al., 1993; Lande, 1994; Lynch & Gabriel, 1990; Poon & Otto, 2000; Schultz & Lynch, 1997; Whitlock, 2000; Whitlock et al., 2003).
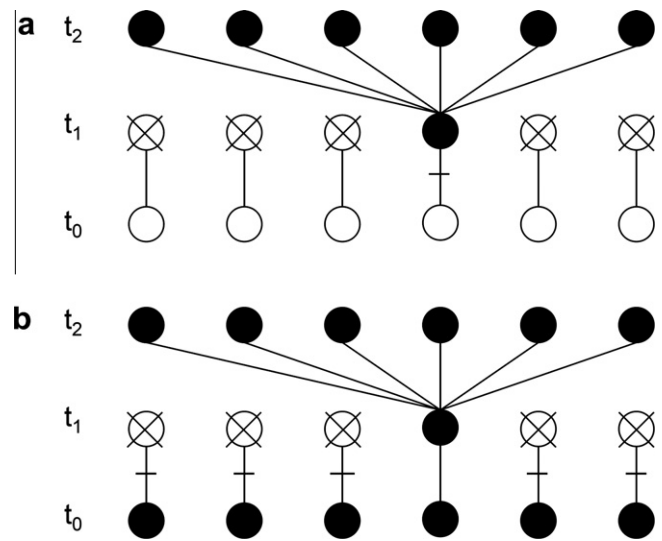
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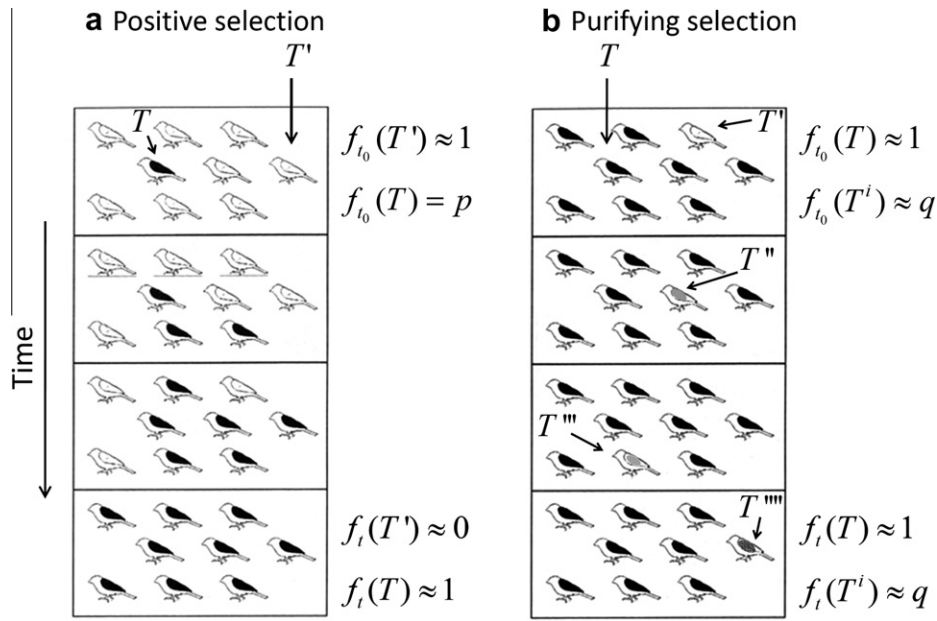
Fig. 3. Example of positive (a) and negative (b) selection processes.

substitution of T is $\frac{1-e^{-2N\cdot p\cdot s}}{1-e^{-2N\cdot s}}$, where N is the population size and p is the initial proportion of the trait in the population.[8] Thus,

$$P(f_t(T) \approx 1 | NS \,\&\, f_{t_0}(T) = p) = \frac{1 - e^{-2N\cdot p\cdot s}}{1 - e^{-2N\cdot s}}$$

On the other hand, the probability of substitution of a neutral trait (a trait that is not affected by natural selection) is p, that is:

$$P(f_t(T) \approx 1 | \neg NS \,\&\, f_{t_0}(T) = p) = p$$

Thus, (3) is true since is easy to demonstrate that:[9]

$$\frac{1 - e^{-2N\cdot p\cdot s}}{1 - e^{-2N\cdot s}} > p$$

provided that $s>0$, i.e., if natural selection acts positively on the trait.[10]

An equivalent formalization could be made for the maintenance of traits. Natural selection cause that a trait T^* is maintained in the population if

$$P(f_t(T^*) \approx 1 | NS \,\&\, f_{t_0}(T^*) \approx 1) > P(f_t(T^*) \approx 1 | \neg NS \,\&\, f_{t_0}(T^*)$$
$$\approx 1) \tag{4}$$

The left term of the inequality is the frequency of a wild-type when the population suffers a mutation pressure of a trait which has lower selection coefficient than the wild-type (and thus, it is constantly purified by negative selection). Another classic result of population genetics is that the disadvantaged trait remains at a frequency of $f(T) \approx \sqrt{\mu}$ in a mutation-selection equilibrium, where μ is the mutation rate of the trait. Thus,

$$f_t(T^*) = 1 - \sqrt{\mu}$$

which is nearly one (unless μ is huge). Therefore,

$$P(f_t(T^*) \approx 1 | NS \,\&\, f_{t_0}(T^*) \approx 1) \approx 1$$

On the other hand, in the absence of natural selection, i.e., if new mutations are neutral, almost certainly the wild-type trait will be eventually substituted by a mutant (Kimura, 1983):

$$P(f_t(T^*) \approx 1 | \neg NS \,\&\, f_{t_0}(T*) \approx 1) \approx 0$$

Thus, (4) follows immediately.

Therefore, these classical results of population genetics show that natural selection can be understood as a probabilistic cause of –and statistically relevant to– the propagation of new advantageous traits by positive selection and the maintenance of traits by purifying selection against new traits.[11]

Note that relation among propagation/maintenance and positive/negative natural selection (NS) is not stipulative. The propagation of a new mutant can be driven by NS but not necessarily (it can be done by genetic drift). Similarly, the maintenance of the wild-type can be caused by negative NS against the new mutants but also can be caused by genetic drift. As a matter of fact, the neutral model of Kimura (1983) shows that the majority of neutral mutants are lost by drift, which maintains the wild-type unchanged by much more time than the expected if mutants were propagated by NS.

From the historical point of view it is important to note that the differentiation between the explanation of propagation and

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[8] Such as in population genetics an allele with a new mutation is considered another allele, we refer to a trait changed by a mutation as another trait.

[9] In fact, the function at the left is monotonically increasing and tends to p as s tends to zero.

[10] Note that the selection coefficient is defined as $s = (W_{mut} - W^+)/W^+$, where W_{mut} and W^+ are the fitness of the mutant and the average fitness of the population wild-type, respectively. Thus, it involves population properties, suggesting the suitability of Millstein's (2006) account of natural selection as a causal process operating at the population level, at least for the explanation of propagation and maintenance of traits (see note 18), where the explananda refer to population properties. For the origin of traits, however, the effect to be explained is the emergence of one individual with a new trait, which can be understood as an individual-level phenomenon (as well as in the explanation of individual existence and trait identity).

[11] From this point of view, to explain the dynamics of trait frequencies in a population over time implies explain the composition of a population at a particular point in time (e.g., that 90% of the population are individuals with trait A and 10% are individuals with trait B), and thus they are not two different explananda, as was recently assumed by Stegmann (2010a).

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maintenance of traits may be considered part of the causes of the Darwinian revolution. The idea that selective natural forces against new disadvantaged variants maintain the status quo of species was widely spread before Darwin's and Wallace's works (Gould, 1982, 2002). Thus, the idea of selective maintenance of the features of species is previous to the development of natural selection theory. The trigger of the Darwinian revolution was Darwin's and Wallace's assertion that natural selection can explain the propagation of changes in species, and thus, the change of species over time (Gould, 1982, 2002). In other words, the core revolutionary idea of Darwin and Wallace was that, while new trait variants being more negative (or less positive) target of selection than the wild-type do not lead to species change, new trait variants being less negative (or more positive) target of selection than the wild-type lead to species change.

4. Explaining the origin of traits

The Non-creative View of natural selection (Table 1) rejects that natural selection can explain the origin of traits in nature. The arguments are of two types: an a priori argument and an empirical argument. First, natural selection only makes sense as acting on an already existent trait, i.e., it cannot influence something that does not exist. Thus, by principle (i.e., by non-empirical issues), natural selection cannot have a causal role in the origin of a trait. A second argument is that natural selection could have an influence over the origin of a trait in the sense that the environment could make "adaptive" or "directed mutations" more probable, i.e. favor mutations that generate a trait with higher probability if it were advantageous in such environment. Thus, according to this argument it is an empirical task to resolve whether or not natural selection influences the production of a yet nonexistent trait. From the empirical point of view, the existence of adaptive mutation is currently discarded, and thus, selective pressures or adaptive situations for future mutations do not influence the production of such mutations (Lenski & Mittler, 1993). This second argument was an important issue in genetics and evolutionary biology (see Lenski & Mittler, 1993 and references therein), but it could be hardly understood from a non probabilistic approach to causation. Contrarily, the probabilistic account can express this fact as follows:

If the formation of a trait T from a previous structure T_0 involves only one mutational change m_* then natural selection is not a cause of nor is it explanatorily relevant to the origin of trait $T (T_0 \rightarrow T)$ because

$$P(T_0 \rightarrow T | NS_T \ \& \ m_*) = P(T_0 \rightarrow T | \neg NS_T \ \& \ m_*) \qquad (5)$$

where NS_T means that the trait T is favored by natural selection (i.e. $s > 0$).

Thus, the probabilistic account of causation allows to formalize the claim that NS cannot explain the origin of one-mutation traits but can explain the origin of complex traits (Huxley, 1943, Ch. VII(7), Forber, 2005; Neander, 1988, 1995a, 1995b). The point of the Non-creative View of natural selection with respect to the origin of traits is well established by Eq. (5) when the trait being studied arises from a single mutation.[12] Nevertheless, the majority of the interesting traits for biology are not structures consisting only of a single variation (i.e., a different phenotype due to

a single genotypic change), but their evolutionary acquisition involves at least more than one variation accumulated over many generations. The major point of the Creative View is that natural selection makes more probable the occurrence of types of sequences of phenotypic steps that seem impossible (in other words, extremely improbable) to occur by the random accumulation of changes. This "creative force" of natural selection has been associated with the ability of natural selection to explain or cause the 'origin', 'formation', 'generation' or 'building' of traits (Table 1 for references). When the origin of a trait T involves more than one advantageous mutation $(m_1, m_2, \ldots, m_n)$, then the probability of this *type of sequence*, with and without NS, should be compared. It is possible to demonstrate that in this case (see Appendix 1):

$$P(T_0 \rightarrow T | NS_T \ \& \ m_1 \cdot m_2 \cdots m_n) > P(T_0 \rightarrow T | \neg NS_T \ \& \ m_1 \cdot m_2 \cdots m_n)$$

Accordingly, the causal role of natural selection for the origination of a *type of trait* can be understood as the probabilistic causation of the type of sequence that forms it. Nevertheless, it is important to emphasize two points. First, the argument asserts that natural selection *can* explain the origin of a trait when it involves more than one advantageous mutation, but it does not assert that natural selection *actually* explains the origin of a trait when it involves more than one advantageous mutation. The second assertion was held by Huxley (1943), who implicitly assumed that it was not possible that two or more advantageous mutations could be substituted by chance. Nevertheless, this cannot be discarded in general in finite populations, and mainly in populations with small or medium size where the role of random drift is important (Crow & Kimura, 1970). Second, the argument indicates that the probability of the *type* of sequences that yield that *type* of trait are probabilized if the probability of this type of sequence is lower in a neutral regime where natural selection does not act. This allows avoiding the possible probabilistic tautology of the following argument: *the formation of whatever trait that requires a particular sequence of steps to form will be probabilized if the sequence is probabilized.* For example, the creationist Behe (1996) has criticized the classical argument for the creativity of natural selection saying that the argument is teleological. According to Behe, the argument assumes the result (a particular trait) and asks the probability of the result if the steps for such result are selected for. Obviously the probability of something is higher if each step to reach it is probabilized.[13] In order to avoid this tautology, the core point of the Creative View could be contrasted with the assertion made by Morgan (1932). Morgan maintained that in the absence of natural selection all traits of the known forms of life would exist along with the many others traits ruled out by natural selection. However, it seems that this is not the case. A proper thought experiment to resolve this point could be a world where all mutations are effectively neutral, i.e., where all new traits do not confer a significantly higher or lower reproductive success to the possessors.[14] Then: What kind of traits would have arisen? The Creative View of natural selection for the explanation of the origin of traits is that the probability that any known trait would have arisen without natural selection is much lower than its probability with natural selection. Thus, the explanatory role of natural selection in the origin of traits could be reformulated by the assertion that the probability that the types of traits observed on the Earth would have arisen without natural selection

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[12] That is true because the previous state T_0 is taken as a given. However, if the previous maintenance of T_0 is required for the mutation m_* to generate the trait T, and if the previous maintenance of T_0 is explained by natural selection, then natural selection explains in part that the mutation m_* generates the trait T.

[13] Note that several metaphoric illustrations of the creative force of natural selection (see note 20) fall in this probabilistic tautology. For example, the tautology of the argument is evident in Simpson (1947) metaphor which shows that to obtain the word "cat" from a pool of letters in which 'every time you draw a *c*, an *a* or a *t* in a wrong combination, you are allowed to put theses desirable letters back in the pool and to discard the undesirable letters... Your chances of quickly obtaining the desired result are improved...'.

[14] The experiment also could be a world where all population sizes are small, such that $|Ns| < 1$ for all mutations (i.e. the effective neutrality of all mutation is always guaranteed).

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is lower than with it.[15] The Darwinism's faith on the 'creativity of natural selection' is supported by the extremely intricate organization and complex order of the structure and functionality of traits whose integration and coordination with environmental cues confer to them the aspect of design, a sign of a type of trait originated by natural selection (and thus are usually called 'complex adaptations'). Nevertheless, it is important to note that at least four other possible scientifically valid and non negligible explanations of these organismal features could be responsible for this phenomenon as well, and therefore the explanatory role of NS in the origin of complex traits cannot guaranteed beforehand.

First, neutral evolution could explain the origin of complex traits. For example Stoltzfus (1999) proposed a model in which complex and intricate traits that 'appear to be adaptations' arise, not by the classical model of beneficial refinements but, instead, by a repetition of neutral steps. Thus she criticized common assumptions like Brandon's (1990, p. 175).

'It is worth noting that presumably no serious biologists think that other evolutionary mechanisms [i.e., other than natural selection], such as drift or pleiotropy, can produce complex and intricate traits that appear to be adaptations.'

In this vein, Lynch (2007a, 2007b) defended the unavoidable role of non adaptive forces of genetic drift and mutation in the explanation of a large set of evolutionary phenomena such as genomic architecture, gene structure, and developmental pathways. Second, it has been proposed that traits with a coordinated stability and order could arise spontaneously in network regulatory systems such as genetic or metabolic systems (Kauffman, 1991, 1993). Thus the central regulatory and organizational features of cell types and cellular differentiation could be the spontaneous result of systemic relations in networks that meet certain basic features, or the by-product of increasing complexity (e.g., the increase of gene number; see Kauffman, 1991, 1993), which in turn could be merely due to passive trends (Carroll, 2001; Wagner, 1996). That is, if gene number increase is a passive non-adaptive trend, and if this is the cause of the major organization of cell types (Kauffman, 1991), then natural selection is not relevant to the explanation of the major organization of cell types at all. Similarly, based on computational algorithms, Wolfram (2002) claimed that natural selection is not necessarily the responsible for complexity in living beings, since simple rules based on local interactions can produce complex structural patterns (Rohde, 2005; Wolfram, 2002). Thus, if relatively simple genetic subprograms could be responsible for individual aspects of organisms, complexity could be the unavoidable result of the random addition of "programs" (rules), many of which happen to lead to complex features (Rohde, 2005; Wolfram, 2002, but see Weinberg, 2002 for criticisms). Third, a similar spontaneous tendency to order is characteristic of thermodynamic systems permanently far from equilibrium (Prigogine & Stengers, 1984). Thus, because living beings are systems thermodynamically far from equilibrium they have an inherently ordered developmental dynamics that cannot be neglected (Brooks & Wiley, 1986, p. 23; Schneider & Kay, 1994). Like the intricate organization and complex order of the structure of the snowflakes, living beings' complex structures could be also explained by the heat flux from

the system to the environment. Fourth, intracorporeal selection has been historically claimed as an agent of structural and functional phenotypic organization (Gould, 2002). Somatic selection (also called 'epigenetic selection' or 'developmental selection') has been proposed as a mechanism that could explain functional patterns without central coordination of elements (West-Eberhard, 2003). Emergent functional properties finely tuned by local adjustments could arise by somatic selection, where spontaneous order or self-organization is the consequence of epigenetic selection processes (Kauffman, 1993; West-Eberhard, 2003, Ch. 3). Recently similar large-scale spatial organization arising epigenetically, not being encoded directly in the genome, has been suggested even for microorganisms or unicellular organisms (Mojica et al., 2009).

Thus, a good challenge for those who defend the role of natural selection in explaining the origin of traits is the suggestion that types of traits similar to those we know could arise in a neutral world by some of the four previous possible mechanisms for the emergence of organized systems or by a combination of them. Nevertheless, this challenge is faced with a long history of skepticism about the possibility to contrast chance with natural selection in the trait formation, which is exemplified by Mayr's words:

When one attempts to determine for a given trait whether it is the result of natural selection or of chance (the incidental byproduct of stochastic processes), one is faced by an epistemological dilemma. Almost any change in the course of evolution might have resulted by chance. Can one ever prove this? Probably never.' (Mayr, 1983).

Interestingly, a new kind of anti-Creative View seems to have arisen (Badyaev, 2008; McShea & Brandon, 2010; Reid, 2007), which apparently does not negate that natural selection *can in principle* explain the increasing of complexity and origin of new traits by the 'linear exaggeration of complex structures' (Badyaev, 2008), as in the artificial selection, i.e. they do not criticize the Creative View in a priori terms. Instead Reid (2007) claims that natural selection *cannot in fact* explain the complexity, trends and diversification of organisms. On the contrary, natural selection must be *relaxed* (i.e., it must not be present) to generate these phenomena (Badyaev, 2008; Reid, 2007, see in this line Wolfram, 2002 and Rohde, 2005). In probabilistic terms, if this were the case natural selection would be explanatory relevant but not a cause of these processes.[16]

5. Explaining the traits identity and individual existence

During the last thirty years of discussions in philosophy of biology two curious metaphysical explananda have been added to the propagation, maintenance and origin of traits. They concern the following issues: Can natural selection explain, for a certain individual, *why that individual has the traits it does*? Can natural selection explain, for a certain individual, *why that individual exists*?

Can natural selection give an account—to some extent, at least—for the traits of individuals? Previous sections would seem to provide us with a rather straightforward answer: yes, of course that natural selection can help to explain the traits of individuals, whenever the traits in question are the result of a cumulative selection process—indeed, as more steps are involved in the pro-

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[15] This thought experiment corresponds to the called 'pan-neutral molecular model' in which all mutations are neutral, but the more realist 'neutral model' includes a significant fraction of deleterious mutations (Kimura & Ohta, 1977; Razeto-Barry et al., 2011). Thus, in an alternative and more significant version of the Creative View the thought experiment would be a world where all mutations are *effectively neutral or deleterious*, i.e., where all new traits *do not* confer a significantly *higher* reproductive success to the possessors. Thus, the explanatory role of natural selection in the origin of traits could be reformulated by the assertion that the probability that the types of traits observed on the Earth would have arisen without *positive* natural selection is lower than with it. If this is the case, purifying selection by itself cannot explain the types of traits observed on the Earth because, as we mention above, purifying selection is not cumulative. Thus, the common analogy of natural selection with a "sieve" (Dawkins, 1986) should be taken carefully.

[16] Note that according to definitions (1) and (2) A is relevant to explain B if and only if A causes B or ¬A causes B. Thus, we interpret Reid's (2007) claim to mean that the absence of natural selection is a cause of the diversification and complexification of organisms, for example, the origin of new niches or the release of ecological resources that relax competition.

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cess by which a given trait arises, greater is the explanatory power of natural selection for it. This is probably the case for your eyes: insofar as yours eyes result from a long evolutionary process, which surely involved very many mutation, propagation and maintenance episodes, to this extent then the natural selection process is involved in the explanation of your eyes.

However, according to certain philosophers things are a little bit more complex that they look at first (Table 2 for references). The issue began some few decades ago, initially concerning certain passages of Elliot Sober's (1984) book *The Nature of Selection*, such as the following:

> 'Natural selection does not explain why I have an opposable thumb (rather than lack one). This fact falls under the purview of the mechanism of inheritance (Cummins, 1975). There are only two sorts of individual level facts that natural selection can explain. It may account for why particular organisms survive and why they enjoy a particular degree of reproductive success. But phenotypic and genotypic properties of individuals –properties of morphology, physiology, and behaviour– fall outside of natural selection's proprietary domain'.
> . . .'The frequency of traits in a population can be explained by natural selection, even though the possession of those traits in the population cannot. This reflects the fact . . . that selectional explanations, unlike developmental ones, do not explain population level facts by aggregating individual level ones. Selection may explain why all the individuals in the room read at the third grade level, but not by showing why each individual can do so'. (Sober, 1984, p. 152)

Karen Neander (1988, 1995a, 1995b), followed later by others (e.g., Nanay, 2005) argued that Sober (1984), preceded by someone and followed by others (e.g., Cummins, 1975; Dretske, 1988; Dretske, 1990) holds a negative view with respect to the role that natural selection can play in the explanation of the adaptations of individuals. Key in the debate that followed is that under the label 'negative view', Neander put together—and sometimes treated as equal—two very different things. The first is *the denial that natural selection can explain how certain types of traits can come into existence*, e.g., how it is that things such as your eyes, which are so tricky and complex, could arise throughout a purely natural process. That is, the first thing that Neander put under the label 'negative view' and attached to Sober and company is the denial that Darwin and Wallace really answered the old question of the origin or "creation" of adaptations, to which the natural theology answers with God, a Divine Designer (Paley, 1802, for a classical exposition) In brief, this is what we have called the 'Non-creative View' of natural selection with regard to the origin of traits.

The second thing to which Neander refers with the label 'negative view' is the denial that natural selection can explain, for a certain individual, *why that individual has the traits it does*, i.e., the denial that natural selection can explain, even partially, why you have five fingers in each of your hands, or, say, why Peter has a heart. Since much of the debate that originated from and followed the publication the Neander's papers was concerned with this question, we called this explanandum the 'trait identity', and the affirmative and negative response to it the Positive and Negative View, respectively (Table 2).

For a while, these two things were being discussed together, thus generating a lot of confusion and misunderstanding until now (e.g., see Nanay, 2010; Stegmann, 2010b). However, since Walsh (1998), it became possible to discern between them with ever increasing resolution. Whereas the Negative View (the second denial) was effectively proposed and supported by Cummins, Sober and Dretske, it is not clear at all that the same goes for the first denial—rather, it seems that Sober simply never considered the origin of traits. Neander, on the other hand, despite arguing vigorously

that natural selection can effectively contribute to explain both the origin of traits and trait identity, mainly made the case only for the first (Neander (1995a, 1995b)).

As things currently stand, we have to consider whether natural selection can or cannot help to explain, for a certain individual, why that individual has the traits it does. The major argument of the partisans of the Negative View is based in the contrastive nature of explanations (Lewens, 2001; Pust, 2001, 2004; Stegmann, 2010a, 2010b). This simply means that when, regarding some aspect, one asks why, one is really asking *why this* aspect *rather than another*. A classical example will be illustrative enough: 'Why did Robert rob the bank?' can be understood in several different ways: (i) 'Why did *Robert*, rather another person, rob the bank?'; (ii) 'Why did Robert *rob* the bank, rather than do something else in it?'; or (iii) 'Why did Robert rob *this bank*, rather than another one or a store, post office, private house, etc.?'

The contrasting context becomes especially important to clarify these explananda. Thus, an explanans must explain both the occurrence of the explanandum and the non occurrence of the contrasting context of the explanandum (a counterfactual situation). It is possible to formulate a probabilistic approach to the contrastative nature of explanations. For example, in the case (iii), if 'the bank is the only place with considerable money in the town' is the explanans (E) that 'Robert robs the bank' (e) rather than 'Robert robs another place in town' (the contrasting context, CC), then the following inequality must be satisfied:

$$P(e|E) \neq P(e|\neg E) \tag{6}$$

(that is, the probability that Robert robs the bank given that the bank is the only place with considerable money in the town is different from the probability that Robert robs the bank given that there are also others places, e.g. the store, with considerable money in the town). But also the following must be satisfied:

$$P(CC|E) \neq P(CC|\neg E) \tag{7}$$

(that is, the probability that Robert robs the store given that the bank is the only place with considerable money in the town is different than the probability that Robert robs the store given that the store also has considerable money in the town).

Now, if we assume this contrastative epistemological framework, the question 'why a particular individual—a—has a certain trait—F—?' can be interpreted in two ways: (i) why the particular individual a, rather than another individual, has the trait F; and (ii) why the particular individual a has the trait F, rather than another trait, say, G. Inasmuch as there are other individuals beside a that have the trait F, the question (i) doesn't look to be of particular interest. On the other hand, if we consider the question of trait identity (ii), with it we enter into certain metaphysical issues concerning personal identity, and in particular, the *origin essentialism thesis*.

The origin essentialism thesis about the individual identity is the thesis that takes a certain fact concerning the origin of an individual to be essential to the identity of that individual. Usually, this thesis is interpreted as meaning that, *inter alia*, I am necessarily the son of my parents, nobody born of other parents could be me. Thus, the parents of an individual are necessary to his identity, so an individual with other parents that his own it is nothing but an impossible metaphysical fantasy—an individual with other parents than he actually has, is a different individual than he actually is; to be the same individual but with different parents is not possible.

The shared argument of the proponents of the Negative View is based in both the assumptions of origin essentialism and genetic determinism (e.g., Pust, 2004, p. 777) (that is, the assumption that specificity of traits is wholly determined by the genetic inheritance of parents and not depends of developmental or environmental conditions of ontogeny). Then it is clear that, under these assump-

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tions, an individual with different traits from the traits he has is an individual with other parents than his own, and therefore impossible. Simply it is not possible, for a certain individual, to have traits distinct from the traits he actually has. This implies that question for trait identity (ii) lacks a contrastative clause, and a fortiori, by the contrastative epistemological framework, that it is not a question at all. Then, for this reason the supporters of the Negative View claim that natural selection cannot explain why particular individuals have the traits they do.

In contrast with previous arguments we claim that although we share the assertion that NS cannot explain trait identity, this is not because the question is nonsense. Instead we claim that trait identity is not explainable by NS because the probabilistic contrastive clauses (6) and (7), although legitimately applicable, are not satisfied by NS as explanans. The reason why trait identity is ruled out as legitimate question by the partisans of the Negative View is because the assumption of genetic determinism. However genetic determinism is an unrealistic and unnecessary assumption given the generality of this issue. Given that traits of individuals can be different because of developmental plasticity or by phenotypic flexibility (Piersma & Drent, 2003), trait identity is a legitimate question that does not lack of contrasting context. Different paths of development or environmental conditions can modify the traits of particular individuals. NS could in principle alter the probability that a particular individual a has the trait F rather than the trait G if NS can modulate the environmental factors to which the development of an individual organism is sensible (see below). The problem with NS as explanatory relevant for trait identity is that in general terms (we will see some exceptions) NS cannot make such a thing. That is, generally clauses (6) and (7) are not satisfied by NS because:

$$P(F(a)|\exists x, x = a \ \& \ NS) = P(F(a)|\exists x, x = a \ \& \ \neg NS) \quad (8)$$

and

$$P(G(a)|\exists x, x = a \ \& \ NS) = P(G(a)|\exists x, x = a \ \& \ \neg NS) \quad (9)$$

where $G(a)$ is the individual a with the trait G and $G \neq F$.

It has to be mentioned that, although generally NS cannot explain trait identity, there are some cases in which NS can modify the environmental (ecological) conditions that determine whether a particular individual a has the trait F rather than another one G. For example, it is well known that the development of inducible defences of preys (e.g., Daphnia) depends of the density of predators in the environment (Jeschke, 2006; Jeschke & Tollrian, 2000; Miner et al., 2005), which in turn can depend of natural selection. Furthermore, inducible defences might depend of the frequency of some trait in the predators, which can be directly dependent of natural selection. In these cases NS effectively can explain why particular individuals have the traits they have (rather than another one).

Note that for the general case (Eqs. (8) and (9)) the contrastive context necessarily entails the existence of the individual for the contrastive clause has sense, which connect us with the last postulated explanatory role of NS. A byproduct of the later discussion was the question of whether natural selection can explain that particular individuals exist rather than do not exist. Because natural selection determines in part which among all possible particular individuals that could have existed and reproduced effectively existed and reproduced (Walsh, 1998), then natural selection can explain the existence of particular individuals.[17] Although we do not know of any philosophical opposition to this idea some problems

could be raised against it. Brooks and O'Grady, 1986 argued that nonexistent items 'cannot be cited in explanations of the etiology of the species which exist' (p. 84) and that arguments of the type 'the frog is green because red, yellow, and blue frogs were devoured long ago' require a "negative space" of "other possible species" which are non-evidential and cannot be taken into account in scientifically acceptable explanations (pp. 84ff). This argument is subsumed under the wide range of discussions about the counterfactual approaches of causality and explanation, and we shall not enter into it. One thing that seems evident is that explanations of the origin of traits and individual existence necessarily involve counterfactuals in order to consider an explanation complete.

Another problem with explaining individual existence is that the contingent and historically specific nature of the genealogical process (meeting, mating, meiosis, fertilization, vital dangers, and so on) makes the individuality of particular organisms extremely fragile (Parfit, 1986). Thus although natural selection could influence the course of contingent facts that probabilize the emergence of organisms with a certain type of traits, its influence on the existence of particular individuals would be quite negligible in light of the strong effect of other contingent factors. So, to consider it as an explanandum of natural selection would be far-fetched. Indeed, in a contrasting context, a probabilistic (statistically significant) estimation of the existence of particular individuals seems implausible.

6. The plurality of natural selection explananda

We have shown that natural selection can be understood as a probabilistic cause. Using other concepts of cause (e.g., counterfactual and the manipulation account), some authors have questioned that natural selection can be understood as a cause at all (Brunnander, 2007; Matthen & Ariew, 2002, 2009; Walsh, 2000, 2002; Walsh et al., 2002). Nevertheless, the theory has been constructed as a probabilistic theory, thus, our analysis may explain why natural selection has been permanently understood as a causal theory among biologists (Hodge, 2001); apparently the implicit concept of cause used in evolutionary biology is the probabilistic causation.[18] The probabilistic formalization of population genetics and the habitual use of concepts such as 'evolutionary force' are a good reflection of the convenience of invoking probabilistic causality and statistical explanatory relevance to account for the natural selection theory.

It may be useful to make a distinction between the theory of natural selection (TNS) and the natural selection (NS). The TNS does not merely claim that NS exists, but also that NS is a causal factor that, in conjunction with a source of inheritable variation, can explain and in fact explains certain types of explananda. As we argued, there are at least four of these types of explananda, so the delimitation and understanding of the TNS requires the specification and understanding of these explananda and how they are related.

The scope of the natural selection explanatory aspirations depends on the relationship between explananda. The explanations of the propagation and maintenance of traits clearly are pre-requisites of the explanation of the origin of traits. Nevertheless, explaining the propagation of traits is not enough by itself, because if a trait is propagated and fixed by natural selection, that does not guarantee that the trait will be maintained over time. For example, an antibiotic resistance could be fixed in a population of bacteria in an environment with antibiotics, but if the environmental pressure ceases (the environment is without antibiotics) the antibiotic resis-

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[17] Thus, the coming existence of individuals and the successful reproduction of its parents refer to the same facts and should not be mentioned separately in explanatory terms (cf. Sober, 1984; Stegmann, 2010a).

[18] For other arguments supporting that natural selection is a causal process, see Hodge (1987), Millstein (2002, 2006), Reisman & Forber (2005), Sober (1984), Stephens (2004), and Shapiro & Sober (2007). Note that this discussion is given only for the propagation and maintenance of traits.

tance very probably will be replaced.[19] In turn, the maintenance of traits has the propagation of traits as a logical requisite. Contrary to the Positive View (Table 2), these explananda do not imply trait identity, which we ruled out as a general explanandum of NS. However, these explananda imply that only a subset of the huge number of possible particular individuals could effectively exist, and thus indirectly they seem to affect (although as one among very many other factors) the probability of the existence of particular individuals. Finally, the origin of traits depends on a cumulative effect of propagation and maintenance of changes, but they must be directed toward some integrative functions or structures, such that the combination of the changes is coordinated into an organized new trait; therefore the explanation of the origin cannot be reduced to the maintenance and propagation of traits.

7. A very brief historical note of natural selection explanda

The idea of selection as a force that preserves the *status quo* (the stasis of species) was common before Darwin and Wallace (including Paley and the natural theologians, see Gould, 1982, 2002). Thus, the maintenance of traits by negative selection is a pre-Darwinian concept. Furthermore, the Darwin's and Wallace's selective explanation of propagation of traits also has some predecessors (as Patrick Matthew (1790–1874) and William Charles Wells (1757–1817), see Gould, 2002). Nevertheless, the explanation of the origin of traits apparently originated with Darwin (and not with Wallace, see Ayala, 2007), and it really begins to be clearly explained with the work of neo-Darwinian biologists, Muller (1929) being the first to explain it in a clear probabilistic form.[20] The current issue about the explanation of trait identity emerged only with Sober (1984) (although with a suggestive anticipation of Nozick, 1974). The explanation of individual existence emerged as a response to the Sober's original claim (Walsh, 1998), but it was further developed by Matthen (1999, 2002, 2003) and Pust (2001, 2004). We see the history of the natural selection explananda as a history of emergence and divergence (differentiation). That is, explananda arise confusedly as a single explanandum and subsequent analyses discover that the issue deals with several distinct explananda.

Acknowledgements

Appendix A

If the formation of a trait from a previous structure T_0 involves n non-epistatic mutations ($m_1, m_2, \ldots, m_n$), then natural selection (NS) is explanatorily relevant to the formation of T* if

$$P(T_0 \rightarrow T|NS \ \& \ m_1 \cdot m_2 \cdots m_n) > P(T_0$$
$$\rightarrow T|\neg NS \ \& \ m_1 \cdot m_2 \cdots m_n) \tag{A.1}$$

where NS means that mutations m_i are selectively favourable (i.e. $s_i > 0$) and $\neg NS$ means that mutations m_i are selectively neutral (i.e. $s_i \approx 0$)

Let us assume that the time between mutations is greater than the time to substitution or loss of fixations in the population. Then (Crow & Kimura, 1970),

$$P(T_0 \rightarrow T|\neg NS \ \& \ m_1 \cdot m_2 \cdots m_n) \approx \left(\frac{1}{N}\right)^n$$

In turn (Crow & Kimura, 1970):

$$P(T_0 \rightarrow T|NS \ \& \ m_1 \cdot m_2 \cdots m_n) \approx \left(\frac{1 - e^{-2s}}{1 - e^{-2Ns}}\right)^n$$

Then, because $\frac{1-e^{-2s}}{1-e^{-2Ns}} > \frac{1}{N}$, (3) is demonstrated.

It is important to mention that it would be a probabilistic tautology to assume that all mutations fixed in the trait formation had positive selection coefficients. Whether this is the case is an empirical, not an *a priori*, matter.

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[19] Indeed, the antibiotic resistance in bacteria has a fitness cost (e.g., Levin et al., 2000; Schrag et al., 1997), furthermore in general if selective constraints are relaxed the trait will be substituted by random mutation and drift (Kimura, 1983, see also Valenzuela, 2000).

[20] It has to be mentioned that, notably, the publications about the creative effect of natural selection (Table 1) lacks a historically aware citation. For example, Ayala (1970), Lerner (1959), Simpson (1947), and Dawkins (1986) have very similar illustrations of the natural selection's creativity, and they are muchlike Muller's (1929) one; however they neither cited among them nor cited the Muller's work. Many in the literature of philosophy of biology cite Ayala (1970) or Dawkins (1986) as the firsts references to the topic, and Stegmann (2010a) referred this issue as a recent one (citing only Forber (2005)).

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