A conceptual taxonomy of adaptation in evolutionary biology

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Introduction

The concept of adaptation is employed in many fields such as biology, psychology, cognitive sciences, robotics, social sciences, even literacy and art,[1] and its meaning varies quite evidently according to the particular research context in which it is applied. We expect to find a particularly rich catalogue of meanings within evolutionary biology, where adaptation has held a particularly central role since Darwin's *The Origin of Species* (1859) throughout important epistemological shifts and scientific findings that enriched and diversified the concept. Accordingly, a conceptual taxonomy of adaptation in evolutionary biology may help to disambiguate it. Interdisciplinary researches focused on adaptation would benefit from such a result. In the present work we recognize and define seven different meanings of adaptation: (1) individual fitness; (2) adaptation of a population; (3) adaptation as the process of natural selection; (4) adaptive traits; (5) molecular adaptation; (6) adaptation as structural tinkering; (7) plasticity. For convenience here, we refer to them as W-, P-, NS-, T-, M-, S- and PL-ADAPTATION. We present the seven meanings in some detail, hinting at their respective origins and conceptual developments in the history of evolutionary thought (references are offered for further deepening). However, it is important to point out that evolution researchers seldom if ever refer to a single meaning purified from the others. This applies also to the authors we cite as representatives of one of the seven meanings. In Discussion and Conclusion draw from our work some future perspectives for adaptation within evolutionary biology.

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[1] We list here some sources from various fields: Eric A. Smith, "Concepts of adaptation", http://courses.washington.edu/anth457/adaptatn.htm (anthropology) — David Sohn, "Two concepts of adaptation: Darwin's and psychology's", *Journal of the History of the Behavioral Sciences*, University of North Carolina at Charlotte, Volume 12 Issue 4, Pages 367 – 375 (a conceptual taxonomy by a psychologist) — Tsang (2005), "Relative fitness and absolute fitness for co-evolutionary systems". *Lecture notes in computer science* [0302-9743] vol:3447 pag:331 -340 (informatics).

Individual fitness: W-ADAPTATION

The term "adaptation" is often used in referring to individual assets, frequently expressed in comparative or superlative forms like "more adapted", "better adapted", "the best adapted" or "the most adapted". This first meaning of adaptation focuses on a single individual and is used to describe particular advantages of it in regard to survival and reproduction. Being about advantage, this is a relative meaning, even if focused on a single organism: individual adaptation results from comparison among organisms of the same local population. The acronym W-ADAPTATION is explained below.

Since Darwin (1859), the comparability of different individual organisms in regard to their ability to survive and reproduce has been a fundamental building block in biology, but it must be said that the technical term "fitness" has gradually replaced adaptation in referring to this meaning. In *The Origin of Species*, Darwin called individuals bearing particular advantages "better adapted" (e.g. 1959 p. 104; 1972 pp. 64-65, 68).[2] Later, Darwin's theory of natural selection has been often identified with the expression "the survival of the fittest", firstly coined by Herbert Spencer (1864), indicating competition among organisms. The mathematical genetic theory of evolution (population genetics) then has been fundamental in consolidating the term fitness, commonly identified by the symbol 'w' – hence we propose the acronym W-ADAPTATION. The British biologist J.B.S. Haldane was the first scientist who quantified fitness in his paper "A Mathematical Theory of Natural and Artificial Selection" (1924), in which he analyzed different cases stressing the direction and the changing rate of gene frequencies.

While developing mathematical models to study the differential success of individuals within a population by natural selection, population geneticists conferred to fitness a "hard" genetic basis: different fitness values were associated to different genotypes (see e.g. Provine 1971). By definition, in fact, natural selection influences the composition of successive generations, and such an influence would be nullified in presence of non-inheritable fitness values. In sum, W-ADAPTATION was definitely grounded on inheritance: individuals are more or less fit according (only) to the genetic features they are provided with at birth.

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[2] P. 104: "But isolation probably acts more efficiently in checking the immigration of better adapted organisms, after any physical change, such as of climate or elevation of the land, &c….", Pp. 64-65: "No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could be still better adapted or improved…" , P. 68: "It may be well here to remark that with all beings there must be much fortuitous destruction, which can have little or no influence on the course of natural selection. For instance a vast number of eggs or seeds are annually devoured, and these could be modified through natural selection only if they varied in some manner which protected them from their enemies. Yet many of these eggs or seeds would perhaps, if not destroyed, have yielded individuals better adapted to their conditions of life than any of those which happened to survive. Ecc."

Each genotype has an *absolute fitness* (commonly identified with the symbol W_{abs}), that is the proportion of the surviving individuals among those born with that particular genotype. Population geneticists usually make reference to the concept of natural selection to define absolute fitness: W_{abs} would be the ratio between the number of individuals with that particular genotype after selection (N_{after}) and the number of those having the same genotype but considered before the action of natural selection (N_{before}):

$$W_{abs} = N_{after} / N_{before}$$

In this way the definition of fitness becomes tightly related with natural selection, and acquires an evolutionary meaning: when the fitness' value is more than 1.0, for example, the genotype is expected to increase in frequency in the following generations; a ratio smaller than 1.0 indicates, instead, a decrease in frequency. A broader vision is obtained by confronting the probability of survival (absolute fitness) of different genotypes within a population. *Relative fitness* – a far more used measure (Wilson 2004) – is quantified as the ratio between W_{abs} of a considered genotype and the highest W_{abs} available in the population (i.e. the fitness of the most successful genotype in the same population). Consequently, the best genotype will be normalized at $w = 1$, and the fitness values of other genotypes are measured with respect to that genotype. Relative fitness can therefore assume any value between 0 and 1 (Orr, 2007. See also Hartl & Clark, 2007). As we have already pointed out, in W-ADAPTATION individual can be considered as the bearer of a particular genotype that is able to determine its survival probability. In the measures of absolute and relative fitness we can notice another implication of the meaning of W-ADAPTATION: genetic sharing. Genotype – and the consequent W-ADAPTATION value – is shared among more individuals, and almost overcomes them with regard to the ontological priority in the evolutionary process.

In population genetics analyses, fitness is seldom attributed to genotypes considered as wholes, but rather to different "alleles" (i.e. different alternatives) of one or few genes. Fitness of a particular allele will predict its frequency in the population in subsequent generations. However, absolute and relative fitness are not necessarily predictive of the evolutionary outcome. Interestingly, studies demonstrate that variation in fitness of single alleles appear to be partly random, and that natural selection will favour alleles with a smaller variance through time, regardless their initial fitness (Hartl & Clark, 2007). So, although natural selection is necessary to define and give importance to W-ADAPTATION, such a process operates at a far larger time scale and in a nonlinear relation with fitness measured in one, two or few generations. Also, we note that W-ADAPTATION can be seen as a cumulate product of different alleles, variously combined.

If fitness has to measure the probability of preservation and diffusion of particular “kinds” of individuals from generation to generation, then such a measure will comprehend a reproductive component besides a survival one. In fact, the success of a particular genotype evidently does not depend only on the high probability of survival it confers to its bearers but also on its effectiveness in enabling organisms to mate (in sexual organisms), reproduce and possibly grow up the highest number of offspring. Thus, the “fittest” individual is also the one who has the highest probability to reproduce and have its offspring spread (and reproduce in turn). Accordingly, there are different ways of quantifying fitness. Some of them include only the ability to develop and survive, others comprehend mating success and fecundity and so on. There is also a measure (*inclusive fitness,* see Hamilton 1964; Coco 2008)[3] that shows how in determinate conditions the sharing of particular genotypes can prevail on the survival of the individual: paradoxically, a self-sacrificing behaviour can be the fittest if it protects several related individuals with a high percentage of genotype sharing (*kin selection*, Hartl & Clark 2007, p. 243). In general, then, survival and reproduction are two rather distinct components of W-ADAPTATION, they interact with each other and can separately be affected by the characteristics of the individual.

By measuring fitness with a panoply of summary statistical measurements, population genetics shows individual characteristics as related to the evolving context of a population, coming to model and predict trends of diffusion of adaptive genotypes and alleles. Population characteristics such as size and genetic composition are relevant. Nonetheless, as the Modern Synthesis reconfirmed in the 1940s (see e.g. Mayr 1997), W-ADAPTATION is characterized by a focus on the organism, its capability of surviving and reproducing in comparison to its conspecifics in a particular ecological context. We may have not stressed enough this latter aspect: fitness has to be considered a value that is always relative and extremely sensitive to a given context, made for example by physical and climatic conditions,[4] amount and structure of available space, cohabiting species which can create phenomena such as e.g. mimicry, or symbiosis, or commensalisms, parasitism, or classic competition for food resources. All these aspects are susceptible of continuous and important changes, and what is favoured in particular conditions may not be such elsewhere. Although quantified in the internal variation of a population, W-ADAPTATION would properly take into account an infinite multiplicity of contextual influences, as the Modern Synthesis emphasized by applying the model of population genetics in ecological, natural contexts.

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[3] Recent paper: Wenseleers T, Ratnieks FL, Billen J., “Caste fate conflict in swarm-founding social Hymenoptera: an inclusive fitness analysis”*, J Evol Biol.*, Jul;16(4):647-58, 2003.

[4] A classical textbook example is the melanism of the peppered moth *Biston Betularia*.

Adaptation of a population: P-ADAPTATION

A second meaning of adaptation focuses on the fact that each species appears to be "well adapted" to its particular life conditions. Modern evolutionary biology has adopted the term *population* to address all conspecific organisms inhabiting a local context (e.g. Jonkers 1973; Ghiselin 1969, 1997[5]; Mayr 1991), so we refer to this meaning as P-ADAPTATION. This is probably one of the most classical meanings of the term, dating back to natural philosophers and theologists who lived and worked before Darwin, as it reflects the traditional idea of order and perfection of nature (e.g. Charles Bonnet, Georges Buffon, see Bowler 1973). *The Origin of Species* inherited the idea of a world in which every organism is perfectly adapted to its environment and to other organisms (Darwin 1859, pp. 60-61, 139).[6] Yet, Darwin's work eventually transformed P-ADAPTATION in an ever suboptimal condition, in which adaptation of populations to environments is always susceptible of improvement through a process (i.e. natural selection) acting on constantly renewed variations.

After Darwin, population genetics re-described P-ADAPTATION in genetic terms thanks to a new model called "mendelian population", considering all genetic combinations of a population with their respective adaptive values and mode of transmission. Sewall Wright (1930, 1932) proposed a particularly influential way of representing the condition of adaptation in a population: fitness landscape – sometimes (yet controversially, see e.g. Gavrilets 2004) called adaptive landscape. This model depicts population as moving across a landscape of genetic combinations with "adaptive peaks" (i.e. the best available genetic combinations in a given environment) and valleys. A population can find itself in different P-ADAPTATION conditions: for example, in equilibrium upon a local adaptive peak; or climbing upon a more or less steep cline; it can also be on the bottom of a valley, risking extinction, and its capability to climb out will rely to an extent on its genetic variation. Even when the population rests on an adaptive peak, P-ADAPTATION turns out to be a "moving equilibrium" rather than a status acquired once for all: wide stochastic oscillations in the population's genetic composition are always present; moreover, adaptive landscapes are influenced

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[5] Ghiselin (1997) claims that the term population is best understood as «a group of things which interact with one another».

[6] Pp. 60-61: "We see these beautiful co-adaptations most plainly in the woodpecker and missletoe; and only a little less plainly in the humblest parasite which clings to the hairs of a quadruped or feathers of a bird; in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world.", P. 139: "It is notorious that each species is adapted to the climate of its own home: species from an arctic or even from a temperate region cannot endure a tropical climate, or conversely. So again, many succulent plants cannot endure a damp climate. But the degree of adaptation of species to the climates under which they live is often overrated."

by environmental changes as well as by other species[7] living therein; accordingly, a peak can always migrate forcing population to an "adaptive pursuit". The single population mapped on an adaptive landscape can find itself divided into sub-populations: they take part in the adaptive dynamics since they can occupy different adaptive peaks and move into an overall dynamics thanks to genetic interchange (gene flow). All these aspects highlight that P-ADAPTATION could not be adequately represented by limiting focus on individuals and environment: it is a distinctive feature of population, and relates to population characteristics such as distribution, size, genetic composition and so on.

According to some models (Hamilton 1964; Wilson & Sober 1998), P-ADAPTATION of a sub-population can include social structure and behaviours, such as altruism. These characteristics would in fact confer some advantages to a sub-population among others. The meaning of P-ADAPTATION can include such aspects that, if relying on individual behaviour, manifest their effect in differential success success among sub-populations (Hartl&Clark 2006, chp. 5.6) (in addition to requiring population features like size, frequency and so on).

An important concept for the characterization of P-ADAPTATION is ecological niche. In pre-darwinian descriptions it was already evident that populations are adapted to environment in a specific, non-generic fashion: all their characteristics seem to fit to a particular position in the environment, defined by food resources, habitat, lifestyle, possible commensalists and others (Darwin 1872, p. 38).[8] In Modern Synthesis, P-ADAPTATION has a sense relative to a particular ecological niche, and niches exploit an important role in evolution and speciation (Mayr 1963 p. 342; Ludwig 1950; Peterson et al. 1999; Beltmanab et al. 2004).

Some approaches point out another dimension of P-ADAPTATION: it does not only concern the relationship between population and its environment, but also population's internal coordination which ensures its cohesion and persistence through generations. Ronald Fisher (1930), for example, pointed out sexual selection as a process leaning toward maximization of prolificacy and mating coordination between sexes within a population. He described this process in genetic terms, claiming that genes were to be considered both as agents of selection (genes manage sexual

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[7] In 1973 Leigh Van Valen proposed the "Red Queen Hypothesis", i.e. the metaphor of an evolutionary arms race where species can maintain their position only by constantly changing, in a context where natural selection indefinitely improves all other species as well.

[8] The geographical races or sub-species are local forms completely fixed and isolated; but as they do not differ from each other by strongly marked and important characters, "there is no possible test but individual opinion to determine which of them shall be considered as species and which as varieties." Lastly, representative species fill the same place in the natural economy of each island as do the local forms and sub-species; but as they are distinguished from each other by a greater amount of difference than that between the local forms and sub-species, they are almost universally ranked by naturalists as true species (Darwin 1972, p 38).

preferences) and as selected objects (genes make sexual ornaments). Sexual selection and natural selection often have different or even opposite directions. Consider the example of peacock's tails: sexual selection would tend to make it more and more colourful and long, with an according shift in female preferences (Miller 2000). On the other hand, natural selection would oppose to the survival of organisms bearing too expensive tails. So, P-ADAPTATION is to be considered a kind of trade-off between the optimums in survival and reproductive terms. In order to maintain its P-ADAPTATION, population has to keep the best possible relation with its environment and also the best possible coordination among its members.

The process of natural selection: NS-ADAPTATION

In evolutionary biology, species are sometimes considered able to "adapt" or "adapt themselves"[9] to their environments (adaptation is actively undertaken by species). Other times, it is said that the force of natural selection "adapts" species (they undergo adaptation passively). In both cases adaptation is used as a verb, and considered as a process of change. The idea that adaptation can be assimilated to the process of natural selection itself dates back to Darwin, and it leads us to name this particular meaning of the concept NS-ADAPTATION . In *The Origin* adaptation is employed as a process only assuming the point of view of natural selection, i.e. a mechanism that "adapts" structures and organisms in order to let them fit better with their environments (Darwin 1859, pp. 86-87, 472).[10]

In order to better understand the meaning of NS-ADAPTATION, some dimensions are particularly relevant: besides the active/passive binomial, we have to consider the relationship between natural selection, adaptation and evolution, the efficacy of selection, and the debate upon the units and levels of selection.

The two terms composing NS-ADAPTATION can be made equal – and also coincident with the evolutionary process as a whole – by a vision which constitutes an extreme position on the first dimension. Such a vision represents natural selection as an active modifying force able to mould species and their structures, and adaptation as a reliable and exhaustive description of what happens

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[9] Examples in recent papers: Ehlers B., Thompson J. (2004), "Do co-occurring plant species adapt to one another? The response of *Bromus erectus* to the presence of different Thymus vulgaris chemotypes". *Oecologia*, Volume 141, Number 3, pp. 511-518(8). Hunter P. (2007), "The human impact on biological diversity. How species adapt to urban challenges sheds light on evolution and provides clues about conservation", *EMBO reports* 8, 4, 316–318.

[10] pp. 86-87: "Natural selection will modify the structure of the young in relation to the parent, and of the parent in relation to the young. In social animals it will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change."; p. 472: "As natural selection acts by competition, it adapts the inhabitants of each country".

in evolution. Julian Huxley offers an example in his *The Modern Synthesis* (1942), where he claimed that in each generation all the individuals who survive beside the elimination process are *de facto* adapted, coming to state that “adaptation is omnipresent” (trad. it. p.375, pp. 63-64).[11] In the 1960s many evolutionists began to express discomfort in regard to the pervasiveness of the notion of adaptation in evolutionary biology, in particular to the habit of constructing adaptive stories as explanations of practically all traits. Consequently, they tried to conceptualize in a different way the relationship between NS, ADAPTATION and evolution. In his book *Adaptation and Natural Selection* (1966), George Williams claimed that not all the effects an organism benefits from are to be explained in terms of adaptation: many of them, in fact, can be due to pure physical laws or can be fortuitous effects. He fostered, then, a return to a concept of adaptation focused on genetic level, the one that was originally formulated by the Modern Synthesis: a process in which changes in gene frequencies are influenced by natural selection. Following this statement, natural selection and adaptation are still coincident, but only adaptations with known genetic basis are to be considered valid, since natural selection acts on gene frequencies (and can be revealed by them); all other effects that result beneficial for organisms are not to be called adaptations. So, ADAPTATION is still equal to NS but they are not exhaustive of the evolutionary process. In 1982, Stephen Jay Gould and Elisabeth Vrba coined the term “exaptation” to stress the fact that natural selection can preserve structures for functions which are not the original (adaptive) ones. Here, natural selection is seen as capable of acting not only through functional adaptation, but also by other mechanisms. ADAPTATION is no longer identified with NS: in evolution structures could repeatedly change the primary functions they are selected for – a process recognized by Charles Darwin (1872) and later named ‘preadaptation’ – or emerge for structural and/or historical causes being later coopted for some function.

We have shown with these examples that different positions are possible about the relationship between the two terms composing NS-ADAPTATION. The question is still open in contemporary evolutionary biology, and different alternatives are present. On the contrary, there is unanimous and long-dating agreement – supported by plenty of empirical research – that non-adaptive and non-selective processes constitute an important part of evolution (e.g. Futuyma 2005 chp. 10; Ridley

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[11] “In ogni momento c’è una costante pressione della selezione, e se il materiale grezzo su cui essa opera è costituito da mutazioni piccole […] l’alterazione principale dello stipite sarà causata dal tratto di riproduzione e sopravvivenza lievemente più basse dei tipi che, benché ampiamente adattati, non sono adattati in grado così elevato come gli altri. Così per la maggior parte la costituzione del gruppo vivente […] cambierà per mezzo di un aumento graduale dei tipi più altamente adattati in confronto a quelli meno altamente adattati e, non per mezzo della selezione dell’“adattato” contro il “non adattato”.

2004 chp. 6-7; Gavrilets 2004; Golding 1994; Kimura 1983). In our words, the evolutionary process definitely does not coincide neither NS nor ADAPTATION.

Another dimension concerning NS-ADAPTATION is the one about the efficacy of natural selection (Gould 2002). Stephen J. Gould, Richard Lewontin (1979) and colleagues have been among those who criticized the view of natural selection as an optimizing agent. According to these authors, to consider natural selection as an omnipotent optimizing process is equivalent to deprive it of its very essence, i.e. conservation of the best alternatives among the available variations. As Ernst Mayr observed, in evolutionary biology selection is a process of elimination (2004, pp. 134-135). So, even admitting that natural selection is the main process in evolution, it has to deal with the material available from time to time. In "The Spandrels of San Marco" (1979) Gould and Lewontin claimed that organisms' constraints are particularly important in influencing the direction of the evolutionary process. According to them, natural selection is not strong enough to mould each trait. Rather, organisms are interpreted as the best structural compromises among different demands (not only selective pressures but also various kinds of historical and architectural constraints). This seems to be a reformulation of the above-mentioned active-passive dimension evoked by expressions such as "species adapt to": organisms have an active role in evolution since they limit the power of natural selection through their internal constraints (and this active role must not be misinterpreted as something depending on organisms' active choices or intentional behaviours). On the other hand, the NS-ADAPTATION process has a more passive nature since its moulding efficacy consists in long-term sorting and ratifying. Exaptation (Gould & Vrba 1982) well expresses the active-passive interplay between organisms and NS-ADAPTATION: architectural contraints can give rise to "spandrels" (i.e. structures emerging with no particular functional value) which natural selection can creatively ("actively") coopt for some use. This 'type II' exaptation (functional cooptation by non-aptation) joins 'type I' (functional shift) in depicting NS-ADAPTATION as a creative process acting in a context of constraints. Approaches emphasizing a more properly active role of organisms do exist. Advocates of Niche Construction theory, for example, point out that species can directly modify the context they live in (particularly with abilities such as dam construction in beavers) and consequently – although in an indirect way – selective pressures acting upon them (Odling-Smee et al. 2003). But such an active modification is not necessary in order to recognize an active role to organisms: they participate with their structural constraints in channelling the evolutionary process.

As a last dimension relevant to NS-ADAPTATION we cannot but mention the debate on the objects and levels of selection. Building on previous ideas by Hamilton (1964) and Williams (1966), Richard

Dawkins (1976) proposed genes as the fundamental unit of selection because they are conserved through generations. Such a view has been criticized by those who argue that genes are not directly visible to natural selection (e.g. Sober and Lewontin 1984); selection in fact cannot pick straight among genes but must select among packages created by and containing these and other genes (e.g. organisms). As far as the Darwinian process of natural selection is concerned, the debate is resolved: the unit is the organism and the replication and diffusion of genes are considered as consequences (Sober 1984a; Mayr 1997), but attention on gene replication shed light on possible cases in which selection seems to choose among genes directly (intra-genomic conflict, meiotic drive, see Burt & Trivers, 2006). So, it seems that selective processes *can* happen at levels below the organism. For what concerns higher levels, recently formal models of within-population group selection have been developed (Wilson 1975; Wilson and Sober 1989): selection is considered as the mechanism occurring when a single breeding population is temporarily broken up into sub-groups. The hypothesis is being tested through theoretical and empirical research (Keller 1999) frequently headed with the definition multi-level selection (MLS, Okasha 2006). Other theories about processes of selection taking place at even higher levels have been proposed as well (e.g. Eldredge & Gould, 1972; Eldredge 1985; Vrba & Gould, 1986; Gould, 2002; Gould & Eldredge, 1988). The possibility of multi-level selection opens two considerations about ns-adaptation. Firstly, it is not clear if adaptation can be described only at one level or if it necessary to consider each level independently. Secondly, adaptation at a particular level is more or less importantly influenced by processes happening simultaneously at different levels (e.g. Gould & Lloyd 1999).

Adaptive traits: T-ADAPTATION

Often we can find the concept of adaptation used to point out particular traits (a single structure, or behaviour). Accordingly, it can be used in the plural form: adaptations. We refer to this use of the term as T-ADAPTATION. Darwin himself used the term in this sense (1859, pp. 60-61). Actually, the habit to describe single traits making it evident their adaptation to particular «offices» (e.g. the eye for vision) was engrained in the tradition of natural theology (Paley 1808, e.g. pp. 73, 484).[12] For Darwin, naming particular traits “adaptations” appears to be of current use. Adopting this focus of

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[12] p. 73: “if the utility of vision to the animal which enjoys it, and the adaptation of the eye to this office, be evident and certain (and I can mention nothing which is more so), ought it to prejudice the inference which we draw from these premises, that we cannot explain the use of the spleen?”; p. 484: Eating is necessary; but the pleasure attending it is not necessary: and that this pleasure depends, not only upon our being in possession of the sense of taste, which is different from every other, but upon a particular state of the organ in which it resides, a felicitous adaptation of the organ to the object, will be confessed by any one, who may happen to have experienced that vitiation of taste which frequently occurs in fevers, when every taste is irregular, and every one bad.”

analysis, scientists consider organisms as collections of traits, and traits as entities with autonomy of their own. In this framework, adaptation can also be used in order to distinguish among traits: adaptations are just *those* structures and characters of an organism in which the correspondence and the harmony between structures and conditions of existence are particularly evident. More recently, specific traits have been called genes since endowed with a supposed genetic basis, but the details of such an underlying basis are seen as not necessary for the analysis remaining then almost unknown.

Ronald Fisher (1930) focused in particular on some specific sexual traits that are male ornaments, studying sexual selection as a parallel process to natural selection (see also Miller, 2000). He identified the existence of traits considered as indicators of well-being: male sexual ornaments (e.g. brilliant plumage) conveying information to females about males' fitness which is supposed to be related to "good genes". Sexual ornaments are traits. Female sexual preferences adapt themselves to male sexual ornaments and vice versa. Sexual preferences and traits as well result from a trade-off between selective pressures and female sexual preferences. The fisherian framework points out, T-ADAPTATIONS not only in the relation between organisms and environment, but also in a particular kind of coordination between the organism and all the other organisms composing the population itself. The existence of a T-ADAPTATION can be explained through one, the other, or (more often) both aspects.

For population geneticists, selective pressures acting on a particular trait can be quantified by measuring its frequency in the population, and comparing such measure with the frequency expected in absence of natural selection (e.g. Hardy-Weinberg equilibrium, see Hartl&Clark 2007). A trait, whose frequency exceeds the one expected in absence of selection, will be called T-ADAPTATION.

In his systematization of Modern Synthesis, Julian Huxley (1942) has emphasized the notion of adaptation and the role of traits so much that adaptation is seen everywhere in living beings: everything we find in the living world has to be adapted and traits always enable individuals to increment their fitness. According to this statement (adaptation is everywhere), T-ADAPTATION comes to lose the ability to discriminate among traits which it had acquired in Darwin and Fisher. Actually, the majority of positions within Modern Synthesis (Ernst Mayr, George Simpson, Theodosius Dobzhanksy) stressed non-adaptive aspects of evolution.

William Hamilton (1964) proposed a radical and fundamental shift in the evolutionary explanation: the attribution of fitness to a single allele rather than to the whole genotype. The drive to the elaboration of the so-called "gene's view" came from seemingly maladaptive traits. Hamilton focused his attention on unselfish behaviour, a trait that is in apparent opposition to the "struggle for existence" among organisms, i.e. the mechanism of natural selection. According to Hamilton, since altruism exists, then it must have been positively selected for (i.e. it has to be a T-ADAPTATION). In order to explain this trait, that is *prima facie* unlikely, Hamilton coined the neologism "inclusive fitness", i.e. the fitness one organism expresses in the form of offspring carrying its own genes. In Hamilton's model, the evolutionary process ultimately depends on leaving in a population as many copies of the individual's genes as possible. The question leading Hamilton's studies is: what is the adaptive value of altruistic behaviour? The methodology adopted, then, consists in counting the probability each trait has to be reproduced and to survive in the following generations. An altruistic behaviour can have a high probability to reappear in the following generations if an organism – through such behaviour – helps close relatives (likely, bearers of the same trait) to survive. Each trait is related to a particular gene and, consequently, T-ADAPTATION can be studied in regard to a particular gene, expressed as phenotype traits. A more radical "gene's eye" view has been proposed by Richard Dawkins (1976). He extremized the protagonism of traits: they seem to be the main actors of the evolutionary process. Since the beginning evolution is described as a competition among replicators, i.e. what we currently call genes. These replicators build organisms (vehicles) with the only aim of generating as many copies of themselves as possible, and are expressed in the phenotype as T-ADAPTATIONS.

George Williams (1966) in his book *Adaptation and Natural Selection* pointed out that not all the effects that are benefits for an organism are to be called adaptations, and he fostered a return to the concept originally formulated by the Modern Synthesis and based on population genetics: a concept thanks to which one can discriminate among traits (T-ADAPTATION and non T-ADAPTATIONS).

In a similar way, Gould and Lewontin (1979) highlighted that organisms are rich of traits that have not an adaptive origin, but rather can arise as by-products and side-effects through the organisms' architectural constraints; on the other hand, useful traits are not necessarily to be called adaptations**.** Gould and Vrba (1982) went further proposing the neologism "exaptation" to address alternative mechanisms to explain useful structures. The introduction of the neologism "exaptation" seems, then, to propose a classification in which different traits can be considered and labelled as T-ADAPTATIONS, non-adaptations or exaptations. In thus respect, even if Gould & Vrba assume that organisms have to be studied and considered as inseparable wholes – traits influence each others in complex and intricate ways – they seem to fall back to an idea of separability and classifiability of traits, necessary and favourable theoretical context for T-ADAPTATION.

Recently, advocates of Niche Construction such as John Odling-Smee, Kevin Laland and Marc Feldman (2003), focused attention once again on particular traits which they call "niche construction" traits. They are supposed to let populations modify to a significant extent the environments they live in. Such traits, while being T-ADAPTATIONS (i.e. traits preserved by natural selection for their positive contribution to fitness), end up to modify selective pressures that act on organisms themselves.

Molecular adaptation: M-ADAPTATION

In recent years, new and powerful molecular tools enabled scientists to collect DNA strains in a fast and highly specific manner, and to determine sequences. Studies have given evidence in support of natural selection (Golding, 1994), and have allowed to construct more and more wide and detailed phylogenies. Molecular biology gave support to the Darwinian theory of evolution, to an extent that Darwin could not even imagine. But for molecular biology to become relevant in the study of adaptation, a molecular access to phenotype was needed: in other words, the biochemical (phenotypic) aspect of molecular adaptation (M-ADAPTATION) was to be studied. In the '90s advanced studies in this field have been made possible by new techniques: site-directed mutagenesis can be used to engineer proteins, and functional effects of each and every amino acid replacement can be studied in vitro. Advancements in molecular biology have opened the possibility to study structures which link in a quite straightforward way genetic basis, (adaptive) function and phylogeny. This is the case of proteins for instance. These macromolecules participate in virtually every process within cells and, often working together, achieve particular tasks and functions. A protein is formed by a sequence of amino acids, which determines its three-dimensional structure and its functionality. In a classical study, Perutz (1983) described how the function of hemoglobin relates to its three-dimensional structure. Comparing hemoglobins from various species, he was able to locate few amino acid replacements responsible for its different structure and functionality. Since the sequence of amino acids in a protein is defined by the sequence of a gene, it is clear how much gene-structure-function are here tightly linked. Contact with phylogeny is straightforward when we consider that, quite commonly, gene lineages are studied and used to assess relatedness between taxa.

Organisms living in extreme conditions are often said to have peculiar adaptations. The genetic basis of such adaptations and the molecular evolutionary mechanisms responsible for their presence are just supposed, remain unknown. Studies in molecular adaptation can link phenotype and genetic basis. A typical example could be the bar-headed goose (*Anser indicus*) that migrates over Mount Everest at altitudes exceeding 9 km, where the partial pressure of O_2 is only 30% of that at sea level. The high affinity of its hemoglobin for O_2 (in presence of other substances) can be seen as a M-ADAPTATION to vigorous exercise in such a rarefied atmosphere. Several studies (Perutz, 1983; Asakura et al. 1976; Amiconi et al. 1989; Zhang et al. 1996) identified an amino acid substitution (unique among birds) which is responsible for the weakening of some bonds in the protein structure, shifting it to the high-O_2-affinity state. The Andean goose (*Chloephaga melanoptera*), which lives 6 km high in the Andes, also has a high-O_2-affinity state hemoglobin, but studies showed that the similar structure arises from different amino acid substitutions (Heibl, Braunitzer & Scheeganss 1987). Adaptive convergence in species which are not closely related is here demonstrated thanks to a molecular approach which integrates genotype and phenotype.

Protein engineering can also be used to reconstruct phenotypes of common ancestors of proteins, grouped in classes and families and recurring in different species. Chandrasekharan et al. (1996) reconstructed an ancestral enzyme (a chymase) from the inferred genetic sequence starting from a phylogenetic analysis of the sequences of different mammal species. The inferred ancestral sequence was very different from modern sequences, and the entire gene was synthesized chemically. Nevertheless, the reconstructed enzyme was highly active and efficient. Moreover, this study allowed researchers to clarify that the narrow specificity of some modern enzymes is an ancestral state, and the broader specificity of – for example – the rat β-chymase is a derived state. As Golding & Dean (1998) commented, "these results demonstrate the power of combining phylogenetic inference in reconstructing ancient phenotypes with protein engineering, and provide an interesting example of evolutionary degeneration – a specialized enzyme evolving a broader substrate specificity" (p. 357). Accordingly, these M-ADAPTATION approaches can spread light over mechanisms through which adaptation happens in evolution.

Golding & Dean (1998) summarized the molecular study of adaptation (combining phylogeny, protein anatomy and engineering) in the following way: "Most often, we examine sequences that diverged thousands or millions of years ago, in which a substantial number of substitutions have accumulated. Many may be neutral. Others, although selected, could simply be treadmill adaptations accrued as populations track ever-changing environments. Although important, they do not alter protein function in a major way. A few represent major adaptations of large effect" (p. 364). Usually, such major M-ADAPTATIONS require just few replacements which can affect protein functionality in unexpected ways.

M-ADAPTATION is by now a wide and fertile field of research, with a variety of methods (e.g. Yang & Bielawski 2000; Yang & Nielsen 2002) applied in the study of the most diverse organisms and molecular mechanisms, and some dedicated journals. It is important to include in M-ADAPTATION, beside protein structure and function tightly linked to the fixed DNA code, also regulatory mechanisms of gene expression (e.g. Schulte 2001): configurations of gene expression can be an important component of adaptation to the environment.

Many ongoing studies are showing a wealth of evolutionary pathways through which adaptive evolution can take place at the molecular level. A peculiarity of M-ADAPTATION is its ability to reduce the gap between genotype and phenotype, with a consequent greater consistency with phylogenetic reconstruction. We may characterize this approach as "bottom-up" since it focuses primarily on structures in order to study related functions, in opposition to other research strategies in which phenotypic "adaptive" traits (see T-ADAPTATION) are often endowed with a theoretical, presumed, unknown genetic basis – more tractable with mathematical tools. Paradoxically, this new approach of study makes more and more possible to substantiate the tension by Williams and others advocates of T-ADAPTATION to study the organism at the genetic level, and to recognize the function and the role of the single gene or the single genetic feature in the context of its bearer, by evaluating consequences of absence and possible alternatives.

Structural tinkering: S-ADAPTATION

This meaning of adaptation (S-ADAPTATION) stresses the strong (if more or less concealed) conservation of structures throughout evolution and adaptation. Pioneering molecular biologist Francois Jacob (1977) used the term "tinkering" by focusing the idea that "novelties come from previously unseen association of old material. To create is to recombine". For Jacob it was evident that organisms "represent, not a perfect product of engineering, but a patchwork of odd sets pieced together when and where opportunities arose. For the opportunism of natural selection […] reflects the very nature of a historical process full of contingency". Actually, like other ideas mentioned above, this approach dates back to before Darwin, when anatomists and naturalists identified common body plans and deep homologies (e.g. Richard Owen, Georges Cuvier, see Gould 2002). Darwin referred to these studies in many points of his work, speaking about the evolutionary interaction between conditions of existence and unity of type (Darwin 1859, pp. 206, 427-428;[13] 1972, chp. VI). In recent decades the structural approach has been strongly advocated and popularized by Stephen Jay Gould (e.g. 1980, 1989, 2002), and was inherited by macro-evolutionary views in Modern Synthesis and phylogenetic systematics (cladistics). Then, the new science of Evo-Devo (evolutionary biology of development) has given strong empirical support to the conservatism of evolution at genetic and developmental level. In some respects, S-ADAPTATION can be seen as a veil covering real relationships between organisms, as well as the real nature of the evolutionary process.

Cladistics – born in 1950 but spread in '70s – was a set of methods, and also a true critical movement inside evolutionary biology, aimed to bring it back to the basic principles. Cladistics focuses on *affinities* which are *latent* – and, moreover, often *concealed* by adaptations – in anatomical, physiological and behavioural characteristics of living species (Eldredge, 1995; Gee, 1999). Its analyses aim to reconstruct relatedness between taxa (i.e. groups of organisms such as species, or genera, or Families) by considering a great number of shared traits which are of high phylogenetic significance – that is, their diffusion is probably due to common descent. Adaptive characters are not particularly revealing: by definition, they are highly dependent and sensitive in regard to local ecological contexts and their changes. An extreme example of the unreliability of adaptive traits from the cladistic point of view is the adaptive radiation, i.e. a frequent event in evolution consisting in the differentiation of a single species or a single group into several forms, with peculiar characters adapted to very different niches and conditions of life, in a short time (at the geological scale).

S-ADAPTATION is, for cladistics, not only unreliable but often concealing sister-group relationships, such in the case of adaptive convergence, i.e. the production of similar S-ADAPTATION forms from different ancestors, due to similar ecological conditions and selective pressures. Clades (groups of organisms defined just on a kinship basis) can be defined through a list of shared characteristics:

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[13] p. 206: " […] the adaptations […] being in all cases subjected to the several laws of growth. Hence, in fact, the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type.", pp. 427-428: " […] we can clearly understand why analogical or adaptive character, although of the utmost importance to the welfare of the being, are almost valueless to the systematist. For animals, belonging to two most distinct lines of descent, may readily become adapted to similar conditions, and thus assume a close external resemblance; but such resemblances will not reveal—will rather tend to conceal their blood-relationship to their proper lines of descent. We can also understand the apparent paradox, that the very same characters are analogical when one class or order is compared with another, but give true affinities when the members of the same class or order are compared one with another: thus the shape of the body and fin-like limbs are only analogical when whales are compared with fishes, being adaptations in both classes for swimming through the water; but the shape of the body and fin-like limbs serve as characters exhibiting true affinity between the several members of the whale family; for these cetaceans agree in so many characters, great and small, that we cannot doubt that they have inherited their general shape of body and structure of limbs from a common ancestor. So it is with fishes."

they must be present in all members of the clade and also be inherited by the common ancestor. Of course, inherited traits can be present – in the different descendant groups – in several *modified* forms, such as bear's paw and human hand (or, often, much more different). Form differs according to conditions of life and its variation is *not* important, since unity of type (as Darwin called it, 1859) holds on. For example, scales are primitive versions of fur and feathers, so the term "scales" *includes* fur and feathers. The character "scales" is then useful for defining a group composed of reptiles, mammals and birds.

S-ADAPTATION – in opposition to relatedness – would *not* be *measurable* in any way, neither in the form of resemblance (adaptation as a state, phenetic resemblance) nor in the form of change (amount of adaptative as a process). Cladists argued in fact that adaptation would be nothing more than a narrative framework for paleontology – and a harmful one, since it would lead to a misunderstanding of deep time on the basis of our everyday experience (Gee, 1999). Today, molecular cladistics (often called just "the molecular") is a widespread method: it has undergone an incredible expansion, and there are almost no studies in biology which do not make use of it. Most biologists, however, maintain a more integrate approach and criticize the exclusive concentration on cladograms: biogeography, taxonomy and the study of S-ADAPTATION remain important, even if positively constrained and helped by cladistics (Eldredge, 1999).

Working at a macro-evolutionary scale – like paleontologists do – researchers notice the conservative nature of evolution, using it to infer degrees of relatedness among higher taxa. The paleontologist Stephen Jay Gould wrote plenty of essays in showing the abundance in nature of what he called "the panda principle" (e.g. Gould, 1980), i.e. the inventive cooption of available structures for new functions related to novel ecological contexts. This is the case of the radial sesamoid bone enlarged and used as the best solution available to the pandas for handling their unique food re source: bamboo. Following the same kind of reflection we find "The spandrels of San Marco" (Gould & Lewontin, 1979, see paragraph 3) with the introduction of the "exaptation" concept (Gould & Vrba, 1982, see paragraph 3). These authors developed a portrait of evolution acting as a *bricoleur* since it has to deal with historical and structural constraints that are considered as limiting but also challenging factors in regard to the exploration of evolutionary possibilities. It must be said that structural approaches of research (e.g. D'Arcy Thompson 1942; Stuart Kauffman 1995; Brian Goodwin 1994) adopt different approaches focusing, respectively, on the laws of form or giving more importance to structural rather then to historical constraints. S-ADAPTATION is fully consistent with Darwinian evolution and selection, although some authors have developed it in antidawrinian positions.

In recent years, a new field of research has emerged in order to give more scientific corroboration to the structural approach integrating evolutionary biology and development (Carroll, 2005): Evo-devo,. Stephen Jay Gould is recognized as an anticipator of this discipline, thanks in particular to his book *Ontogeny and Phylogeny* (1977). Studying the molecular mechanisms operating in development, Evo-devo has been able to show that evolutionary novelties and peculiarities result from the modulation of same developmental mechanisms. This modulation seems to be the reason for the huge sharing and high conservation of a “toolbox” of genes. S-ADAPTATION appears more and more as an always renewed reconversion of old structures and mechanims to new functions: although often more evident to our perception, adaptive traits appear to be like wavelets blurring the deep interrelatedness of the most diverse species.

Plasticity: PL-ADAPTATION

As last, adaptation is sometimes found in expressions of the kind “the organism adapts to” or “organisms adapt to”, indicating processes by which the individual, thanks to phenotypic modifications, accommodates to novel circumstances in the course of its life.[14] Darwin did not use the term with this meaning, perhaps to avoid confusion with Lamarckian theories of evolution by use and disuse. In evolutionary biology it has been long recognized (e.g. Wright 1930, p. 146) that using adaptation to address individual, ontogenetic processes of change is misleading: other terms have been coined, among which the more representative is plasticity (Pigliucci 2001). Accordingly, the acronym we propose here is PL-ADAPTATION. In early times there was no specific term to address processes of non-genetic phenotypic variation. In 1949 I. Schmalhausen wrote «The individual adaptability of the organism creates for it a condition of what may be called flexible stability or liability. This condition enables the organism to survive sudden and considerable variations of the external environment to another and even reorganize its structure. Hence, knowledge of the development of the organism’s system of adaptive reactions is very important in

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[14] Examples from recent papers: “‘Early Birds’ Adapt To Climate Change” (*ScienceDaily* May 12, 2008). Makes reference to Charmantier A., McCleery R.H., Cole L.R., Perrins C., Kruuk L.E.B., Sheldon B.C. (2008), “Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population”, *Science* 320 (5877), pp. 800 - 803. — Branicky R.S., Schafer W.R. (2008), “Oxygen Homeostasis: How the Worm Adapts to Variable Oxygen Levels”, *Current Biology* 18 (13), R559-R560. — Mokady O, Loya Y, Achituv Y, Geffen E, Graur D, Rozenblatt S, Brickner I (1999), “Speciation versus phenotypic plasticity in coral inhabiting barnacles: Darwin's observations in an ecological context”, *J Mol Evol.*49(3):367-75. It is a plasticity redeclination in organisms studied by Darwin: Darwin C. (1854), “A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae (or sessile cirripeds); the Verrucidae, etc., etc., etc.”, London Ray Society, London.

understanding the laws of evolution. Finally, the origin of adaptability is an insufficiently studied aspect of evolutionary theory. The Lamarckians based their theory upon the premise of an already existing individual adaptability and did not examine its origin while the neo-Darwinians regarded it as unimportant since they assumed that the results of individual adaptability, being non-heritable, have no evolutionary value» (Schmalhausen 1949, p. 175, cit. in Gottlieb 2001 pp. 126-127). In the following years some processes have been studied and named. Laid in the individual, they are quite distinct and separate from NS-ADAPTATION, even if – as we are going to argue – they have the potential to offer a more complex view of natural selection.

The first and simpler way by which an organism can become acquainted with novel conditions is learning: involving physiological regulation and association of stimuli and behaviours, such form of PL-ADAPTATION is present in the simplest organism.[15]

In studies on phenotypic plasticity, phenotype is seen as a genotypic *response* to environmental conditions. *Reaction norms* are functions describing the variation of such a response in relation to external changes. Many phenotypic traits can have a fixed reaction norm, i.e. tend to be stable irrespective of the environment. Moreover, reaction norms can be selectively sensitive to changes in some variables while not to others. The plant *Arabidopsis thaliana* is a particularly studied model system for plasticity (e.g. Pigliucci 1998; Piglucci et al. 2002): changes in environmental conditions (light, nutrients, water etc.) induce dramatic restructuring of characters of this plant.

At the molecular level, plasticity can be studied in the *epigenetic* modulation in gene expression, where the genetic sequence remains fixed, while biochemical, physiological and behavioural alterations – occurring in response to changes in the environment – modify the expression of a great number of genes during the organism's life. This process is called *acclimation or acclimatization response* (Schulte, 2001).

Learning, plasticity, and acclimation are individual processes, often referred to as adaptive, or PL-ADAPTATION, clearly distinct from population NS-ADAPTATION. Yet, many studies have pointed out that the two kinds of adaptation are related in complex ways.

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[15] Law E., Nuttley W.M., van der Kooy D. (2004), "Contextual Taste Cues Modulate Olfactory Learning in *C. elegans* by an Occasion-Setting Mechanism", *Current Biology* 14 (14): 1303-1308. — Liu L., Wolf R., Ernst R., Heisenberg M., "Context generalization in *Drosophila* visual learning requires the mushroom bodies", *Nature* 400: 753–756. — Colbert H.A., Bargmann C.I. (1995), "Odorant-specific adaptation pathways generate olfactory plasticity in *C. elegans*", *Neuron* 14: 803–812. — Jansen G., Weinkove D., Plasterk R.H. (2002), "The G-protein gamma subunit gpc-1 of the nematode *C. elegans* is involved in taste adaptation", *EMBO J.* 21: 986–994. — Jansen G., Rademakers S., Hukema R. (2003), "Genetic analysis of adaptation to salts in the nematode *C. elegans*". *Society for Neuroscience Abstract Program* No. 595.1. — L'Etoile N.D., Coburn C.M., Eastham J., Kistler A., Gallegos G., Bargmann C.I., (2002), "The cyclic GMP-dependent protein kinase EGL-4 regulates olfactory adaptation in *C. elegans*", *Neuron* 36: 1079–1089.

For a movement of authors, sometimes defined neo-Lamarckists, PL-ADAPTATION becomes at least in part inheritable by multiple ways of inheritance including epigenetic, behavioral and (in humans) symbolic (Jablonka & Lamb 1995, 2005; Avital & Jablonka, 2000). For example, organisms can directly influence the external determinants of their offspring here and now by choosing or changing the environment in which the offspring will develop. Such an influence can be seen as a further, indirect kind of inheritance. Further, epigenetic factors such as DNA methylation and chromatin remodelling, or even host organisms such as symbiotic bacteria – with dramatic effects on phenotype – can become transmitted to the offspring through reproduction and parental care. So, while nuclear DNA sequence remains fixed in the chromosomes throughout the life of an organism (the "central dogma" of molecular biology), acquired characters and PL-ADAPTATION can be inherited by offspring by other ways.

PL-ADAPTATION can also become fixed in the genome, by more indirect ways. The so called "Baldwin effect" is a mechanism, proposed in 1896 by James Mark Baldwin, in which epigenetic factors are to be considered as important as natural selection and concurrent in shaping genomes (e.g. Simpson 1953; Fuller et al., 2003; Shettleworth S.J., 2004). Behavioural changes, due for example to the movement of an organism into a new environment, can be followed by morphological and physiological changes and, accordingly, such ability to change can be considered as a driving force in the evolutionary process itself. Individuals showing a moderate level of phenotypic plasticity have higher fitness than those that do not; without a plastic response, in fact, the population considered as a whole runs the risk of extinction. Plasticity is to be considered the ability that makes possible the appearance of an environmentally induced phenotype, and so it enables organisms to better fit the environment *hic et nunc*, in the course of their life.

Some researchers interested in this aspect of evolution, such as Mary Jane West-Eberhard and Massimo Pigliucci, claim that, for plasticity to be considered a real driving force in evolution, phenotypic novelties have to become gradually assimilated in the genetic repertoire. This mechanism is called "genetic accommodation" and it is related to a process in which a plastic response begins to be expressed also in the absence of the original environmental input (the one that gave rise firstly to the specific phenotypic trait).

West-Eberhard (2003) affirms that all phenotypic novelties arising when a population enters in a new environment are reorganizations of past and ancestral developmental responses to different environmental inputs, instead of depending exclusively on novel inputs. In order to explain the evolutionary origin of all kind of adaptive traits, she proposes a unified model composed of four steps. First, one or more organisms experience novel (mutational or environmental) inputs which give rise to novel traits and then we assist to a reorganization of different parts of the phenotype. Thus, There is a spread of the new variant in different individuals composing a population and, in case the new variant is associated with an increase of fitness, natural selection will favour that specific kind of phenotype. This is the process called “genetic accommodation” (Pigliucci et al. 2006). The process is not straightforward, since for example environment can change among generations and PL-ADAPTATIONS due to phenotypic plasticity may not become fixed at the genetic level. Clarifying criteria for case discrimination is complex.

In conclusion, a deep analysis of phenotypic plasticity and other ontogenetic processes can lead us to reconsider the complexity of NS-ADAPTATION and help to consider the role played by what happens here and now, at the ontogenetic level. Evolutionary biologists, in fact, are much more used to focus on the phylogenetic or populational level of analysis. According to recent studies, however, it seems important – in order to understand evolution – to consider the novelties coming from the interaction between organism and its environment. It seems, in fact, that adaptive evolution has to be considered a more general process than NS-ADAPTATION. In this framework of explanation, the role played by the interaction between organism and its environment is significant since it influences the evolutionary process itself.

Discussion

1. Compatibilities and incompatibilities among the seven meanings.

In evolutionary biology, as expected, there are at least seven different meanings of adaptation. Among these some incompatibilities as well as some complementarities can be detected.

PL-ADAPTATION, for example, describes the relationship between organism and environment as something flexible: individual genotype is seen as giving different phenotypic responses according to environmental inputs. On the other hand, population genetics describes P-ADAPTATION through a rigid hereditability of phenotypes determined by genotypes. The two descriptions of the relationship between the individual organism and its environment seem to be to an extent incompatible.

Another incompatibility can be pointed out in regard to traits such as altruism, that seem difficult to explain through W-ADAPTATION since they diminish individual fitness. Yet, they are better explained by combining T-ADAPTATION (fitness of the trait) in the context of a population (P-ADAPTATION).

2. Historical origin of the seven meanings.

The reason for diversification of the adaptation concept is clear if we take into consideration the history of biology, where novelties and new fields of research re-declined it without ruling out previous meanings.

Darwin took the traditional meaning of species adaptation as a generalized and perfect state observed in the natural world, and transformed P-ADAPTATION in a suboptimal and relative state while adding the new meaning of individual "degree" of adaptation (later named "fitness", W-ADAPTATION).

By defining the mechanism of natural selection, Darwin paved the way for a conception in which species are seen as involved in an evolutionary process of adaptation to changing environments (NS-ADAPTATION).

The splitting between the PL-ADAPTATION and P-ADAPTATION was possible thanks to the idea of hard inheritance (Weissmann, 1893): population geneticists had already detected the terminological ambiguity (both processes were named adaptation) and begun to use the concept of adaptation only referring to genetically determined traits.

Another achievement of population genetics was the definition and isolation of particular adaptive traits (T-ADAPTATIONS) and their trends through generations in a given population.

S-ADAPTATION has long standing roots but became evident and legitimate in evolutionary biology thanks to the elaboration of cladistic methods, to a higher consideration of the paleontological patterns and to recent discoveries of evo-devo.

As a final example, of course no M-ADAPTATION concept was possible until suitable molecular technologies had been available.

3. Structure/function relationship in the seven meanings.

We recognize a common issue running across all the seven meanings of adaptation: the relationship between structure and function. The relative importance of the two terms can be balanced in very different ways.

S-ADAPTATION constitutes the most extreme position in favour of the importance of structures in evolution: adaptation is seen as the acquisition of new functions in changing contexts.

Other meanings of adaptation have traditionally attributed more importance to function. T-ADAPTATION, for example, tends to recognize and classify traits on the basis of their functions. Correspondingly, in NS-ADATATION natural selection has often been considered as a force able to shape and optimize organisms in a functional way according to the environment they live in.

It seems to us that privileging too much either function or structure in the definition of adaptation leaves the concept incomplete. The most advanced researches, particularly in molecular biology, have been trying to equilibrate the importance attributed to these two elements. Darwin was definitely aware of it (1859, pp. 206-207):[16] adaptive explanations have to be of a structural-functional kind, where structure is related to both phylogeny (historical constraints) and to the morphospace of all the physically possible forms.

4. Levels of descriptions and meanings of adaptation.

Although the concept has been used since Darwin, our analysis shows that several meanings of adaptation exist, and that each of them is preferably used in one of the different fields of biological research. We believe that the roots of such a multiplicity do not reside in scientists' inability or negligence to find a common definition. Instead we note that each concept relates to one of a series of levels of description: molecular level, trait, individual, population and macro (species and higher taxa). We think that this hierarchical arrangement is particularly important in order to reconsider adaptation in evolution, and we will turn back on this topic in the Conclusion. We just recall here the above-mentioned Multi-Level Selection debate as an example of insightful approach integrating entities and processes at different levels of description.

5. State/process dichotomy.

We can outline another dimension by which the concept differentiates: the long-standing state/process dichotomy. Many authors (e.g. Mayr 2004, p. 85; Gould & Vrba 1982) have pointed out that adaptation can mean both a process and its product and that this ambiguity can lead to some theoretical problems. We simply note that two of the seven meanings we listed, i.e. PL-ADAPTATION and NS-ADAPTATION, indicate processes. We can also note that such processes correspond to the same levels of description of W-ADAPTATION and P-ADAPTATION, but the latter two describe the *state* of adaptation in, respectively, an individual and a population. Again, different meanings are not necessarily incompatible but rather they appear to be related to particular research strategies.

6. The importance of boundaries in adaptation. The concept of adaptation becomes more and more difficult to define in recent theories such as Niche Construction theory (Odling-Smee et al. 2003) and Developmental System theory (Oyama 1985, 2000; Oyama et al. 2001). The main reason is that the boundaries typically identified between "adapting" entities and their environments seem to fade

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[16] "For natural selection acts by either now adapting the varying parts of each being to its organic and inorganic conditions of life; or by having adapted them during long-past periods of time: the adaptations being aided in some cases by use and disuse, being slightly affected by the direct action of the external conditions of life, and being in all cases subjected to the several laws of growth. Hence, in fact, the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type."

away. Advocates of Niche construction point out that population modifies its environment and, consequently, natural selection pressures. This is particularly evident in traits called "niche construction traits" such as in the beavers' ability of constructing dams. Generalizing this hypothesis, these authors claim that adaptation is a *constructing process* between environment and population. NS-ADAPTATION that indicates natural selection as operating on populational variations seems to be scarcely applicable if population itself contributes in determining selective pressures. On the other hand, the vision of adaptation as a state of equilibrium (present or to be reached) between population and its environment seems to be compromised if we assume that organisms are not passive actors but rather they modify in a significant way selective pressures acting upon them. A similar dissolution of the boundaries between environment and "adapting" entity is evident at the level of description of the organism. DST focuses on different "sources" that, from different levels, influence the development of an organism. Every trait is produced by the interaction of many developmental resources (genetic, environmental, social, cultural and others) and DST does not distinguish between genetic and environmental. The influence of each source is contingent because of the constant feedbacks that construct the characteristics of the organism-environment system. So, genetic information is not the only information transmitted: external environment, cultural and familiar behaviour, for example, contribute to the development of an individual, of its traits and abilities. Several meanings of adaptation are brought into question by DST. For example, W-ADAPTATION becomes difficult to determine, even more if we try to relate it to a genetic basis or genotype. A single trait cannot be considered adapted (T-ADAPTATION) for some function in a given environment, if such environment is co-responsible for the shape of the trait itself. As we have already pointed out analyzing other approaches, the idea of the organism as a collection of traits becomes problematic. In general, it seems to us that the meaning of adaptation resulting from these approaches does not belong to any of the seven meanings we identify nor can it be considered as a new and autonomous one.

Conclusions

Seven meanings of adaptation are present in evolutionary biology: individual fitness (W-ADAPTATION); adaptation of a population (P-ADAPTATION); adaptation as the process of natural selection (NS-ADAPTATION); adaptive traits (T-ADAPTATION); molecular adaptation (M-ADAPTATION); adaptation as structural tinkering (S-ADAPTATION); and plasticity (PL-ADAPTATION). We believe that the catalogue of meanings can be of some use to scholars and scientists employing the concept in other fields of research, especially in cases of interdisciplinary work.

In evolutionary biology we noted that each of the seven meanings is related to a specific level of description and emphasizes adaptation as either a state or a process. None of these meanings appears to be reducible to any other and the interaction among the levels of description seems to be necessary for evolutionary explanation.

Accordingly, we foster a reformulation of adaptation that is able to reflect a multilevel arrangement and state/process duplicity as well as the interplay between structures and functions. Such a concept would hopefully better account for current works integrating different meanings of the term and even ease the contact between meanings showing more incompatibilities.

The criticisms brought forth by theories such as Developmental Systems and Niche Construction do not propose, according to our analysis, a further concept of adaptation. Their merit is to show the importance, in the study of adaptation, of the boundaries existing between the environment and the adapting entities at the various levels. By considering the constructive and movable nature of these boundaries, they suggest studies susceptible to enrich the comprehension of the evolutionary process and to complement the understanding of adaptation.

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