Niche construction and extra-genetic adaptation: their roles as mechanisms in evolutionary change

VICENTE DRESSINO

ABSTRACT. The niche construction concept has triggered much controversy related to its tensions with the natural selection concept and with its potential role as an updated version of the "adaptation" concept. Empirical data are providing evidence of certain explanatory weaknesses in the dominant evolutionary theory. The contributions of extra-genetic adaptation studies, together with epigenetic research ones, are shaping a new scenario in evolutionary explanations. The aim of this work is to analyze the interrelation between niche construction, extra-genetic adaptation and phenotypic plasticity as evolutionary explanatory mechanisms. In this respect, this work may act as a bridge between classical approaches of evolutionary theory and as an alternative perspective based on the reversibility of extra-genetic or physiological inheritance.

KEY WORDS. Evolution, adaptation, extra-genetic adaptation, phenotypic plasticity, niche construction, evolutionary explanatory mechanisms.

Lamarck's and Wallace-Darwin's classical theoretical approaches towards evolution continue to exist (albeit with some changes) until today. Nowadays, Wallace-Darwin's theory, which was based on the predominance of natural selection as the main explanation of evolutionary change, has begun to show some weaknesses against the empirical data that started to arise in the twentieth century. The synthetic theory, inherited from the Darwinian tradition, presented a gene-centered dominance for evolutionary explanations. However, these explanations were developed based on research carried out on eukaryotic organisms with sexual reproduction. All attempts to broaden these explanations to the large world of prokaryotes and viruses (the latter belonging to the Akamara domain) have been unsatisfactory.

Laboratorio de Investigaciones en Ontogenia y Adaptación (LINOA), Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina. / vdressino@gmail.com

Besides, these theoretical proposals began to be remarkably modified with the advent of the "complexity theory" as the large theoretical framework of modern biology. This theoretical framework involves aspects such as chaos theory, biological phenomena lack of linearity, state of non-equilibrium, randomness, biological processes emergence, biological self-organization, and so on. Accordingly, complexity positions itself as a scientific paradigm that enables the overcoming of certain scientificity criteria based on the mechanism, reductionism and determinism of biological processes. Thus, complexity theory is placed as an important paradigm for biological evolution studies, overcoming the classical approaches that were developed two hundred years ago.

Within this context, the proposal of the niche construction theory, and its relation to the adaptation concept, has driven the necessity to reformulate the concepts of adaptation, extra-genetic adaptation, and their interrelationships with niche construction. The aim of this work is to analyze their previous relationships and highlight the links between physiological adaptation and niche construction, considering phenotypic plasticity as a key factor.

ADAPTATION AND THE DICHOTOMY BETWEEN PROXIMATE AND ULTIMATE CAUSES

In the Lamarckian and Darwinian traditions, the "adaptation" concept has been the fundamental basis for evolutionary explanations. This concept has changed over time and has allowed for several theoretical approaches. One of these is represented by the historical or ancestor-descendant use of the natural selection concept, in which the adaptive feature has a genetic origin. Thus, it assumes that the feature that allows for a better environmental adequacy results from a particular genotype that is selected. Likewise, the non-historical proposal is linked to different biological disciplines, such as physiology, ecology, development biology, etc. These disciplines are either not related to the natural selection concept as a necessary and sufficient explanation, or do not require this hypothesis as an explanatory principle.

Without seeking to make an exhaustive analysis of the historical evolution of the "adaptation" concept, we will concentrate on relatively recent categorizations, which are relevant to the objectives of this work. According to Bock & von Wahlert (1965), evolutionary adaptation may be expressed as a "state of being" or as a "process." The adaptive state of being would represent a good correlation between the biological role of the attribute (the feature) and the selective force of the environment. Instead, the adaptation process would be an improvement of this correlation over time. An extended conceptualization applied to physiological adaptation was proposed by Dressino (2005). This author notes that adaptation as a state of being refers to the study of the feature from which its adaptive state is analyzed. That is to say, adaptation as a state of being represents a stage in a sequence of events that leads to the consideration of this type of adaptation as a value for the organism or the population. For example, when we analyze the importance of birds' wings as a favorable adaptation for flying, neither their embryological nor their evolutionary origins are taken into account, only their functional efficiency for flying. On its turn, adaptation as a process is connected to the physiological and ecological processes that originated the feature. In this latter case, embryological origins as well as feature functionality are considered. The previous example shows that when considering the wings' functional adaptation, Hox genes, growth and development processes, metabolic changes, and so froth are considered. Bock & von Wahlert's justification for adaptation is natural selection; meanwhile, Dressino's explanation is founded upon functionality, physiological, epigenetic and ecological principles.

An important perspective on adaptation to be considered—beyond the state of being-process dichotomy—is its complexity, which entails its dynamic nature. This means that the organism-environment relationship is permanent during the organism's ontogeny. This is because, in every open thermodynamic system, the transfer of matter and energy between the organism and the environment never stops. Therefore, the considerations of adaptation as a state represent a methodological approach aiming at facilitating its study in certain sciences, such as paleontology. In summary, if adaptation is a continuous phenomenon that entails a permanent flow of matter and energy with the environment, the consideration of the adaptive state not only loses consistency, but should be adopted as a process.

Moreover, another approach to be consider from the causation perspective is the idea of proximate and ultimate (or remote) causes in evolutionary biology, proposed by Mayr (1961). In the case of adaptation, the remote causes would be given by the evolution of adaptive features throughout a phyletic lineage selected by natural selection (this explanation is compatible with Bock and von Wahlert's proposal). On the other hand, adaptation in the light of proximate causes frames extra-genetic, physiological and epigenetic adaptations, which are not related to natural selection, and are compatible with Dressino's definition (2005).

Mayr's dichotomy between remote and proximate causes was used in biology for more than fifty-six years. However, several objections to this dichotomy put into question its explanatory value. West-Eberhard (2003) stated that this dichotomy implied that the immediate causes of phenotypic variation were not related to the ultimate or evolutive explanation. This assertion partly loses relevance due to current evidence. In this respect, Laland, et al. (2017) proposed the existence of a new approach to causation, called "reciprocal causation," which is related to the "niche construction" concept. These authors asserted that developmental processes could influence the direction of evolutionary change; consequently, the origin of the evolutionary event is ambiguous. Finally, the authors stated that the hypothesis of ultimate causes should also include proximate processes, since biological evolution is concerned with these processes as well. This approach coincides with Noble's (2013) position that all acquired characteristics (not in the Lamarckian sense) can be inherited in a robust and transgenerational manner that contradicts Mayr's and West-Eberhard's previously mentioned assertions.

EXTRA-GENETIC OR PHYSIOLOGICAL ADAPTATION

In general, extra-genetic or physiological adaptation is conceived as the processes by which organisms are adjusted, in beneficial ways, to the diverse environmental factors that induce phenotypic modifications, which are not transmissible to the offspring. This type of adaptation is also related to explanations of proximate causes. However, nowadays, this general definition is being questioned due to the empirical evidence that shows that adjustments can be either temporary or permanent and acquired through short-term or long-term processes during ontogeny. These processes imply structural, behavioral and cultural changes in order to improve functional performance against environmental pressures. If environmental stresses entail physiological adjustments that involve some kind of differential reproductive success in the population, these changes may lead to some genetic differentiation, thus establishing a genetic adaptation (Frisancho, 1996).

It is worth mentioning that, historically, the "physiological adaptation" concept appeared in the nineteenth century with the emergence of Claude Bernard's experimental physiology (1859/1959). This author introduced the concept of '*milieu intérieur*', which was the forerunner of Cannon's "homeostasis" concept (1932). Anyhow, it is during the Second World War when the concept of "physiological adaptation" surfaced in modern sense (Metz, 1995). Physiological adaptation corresponds now to the minimum activity of organic functions, which are regulated by a coordinating system that guarantees metabolism and homeostasis. Moreover, physiological adaptation is deemed necessary and sufficient if it allows for the individual's life subsistence all throughout its existence.

From his side, Lewontin (1978) suggested that adaptation is the change process through which the organism ensures a solution to the problem proposed by the environment. This definition is adjusted to the physiological problem since every change that occurs in an organism trying to adapt to a given environment (altitude, nutrition, etc.) is, ultimately, an attempt to solve the different problems it faces. It is worth mentioning that the concept of "environment" is a very wide one. It involves different aspects (biotic and abiotic) as well as emergent levels, for example, the social environment that arises from the behavioral interrelationships among organisms.

The field of physiological adaptation has two important concepts as "acclimatization" and "acclimation" (Flok, 1966, mentioned in So, 1980). In this sense, "acclimatization" refers to the biological changes that take place during an organism's ontogeny and that reduce the stress caused by climatic changes and other stressing factors. At this point, it is important to mention that if adaptive features are acquired during growth, there is a development adaptation or development acclimatization. Even so, the differences in acclimatization may be due to multi-stressing effects that operate on the phenotype. Instead, the "acclimation" is used on an experimental level, where the organism is maintained under controlled conditions. The stressing factors or variables are individually modified. In order to have a thorough treatment of these differences, see Frisancho (1996).

In general, it can be assumed that a physiological organization plan exists, and that it is composed of the disposition of matter and energy flows in an organism. Adaptations are the devices that carry that plan out and insert it in a particular environment (Marx, 1984). To sum up, the author considers physiological adaptations as "specific solutions" to the diverse environmental stresses that every organism needs in order to live and maintain and reproduce its form. In fact, adaptation should not be thought of as an isolated or independent phenomenon, but as a synergy of adaptations in different adaptive levels. In short, every adaptation is, to some extent, an *adaptation to the adaptation* more than an adaptation to the "environment" (Marx, 1984). This perspective coincides with the "concatenation of adaptations" concept, which recognizes the existence of multiple adaptations that are linked with each other. The modification of any of those adaptations could have serious consequences on the rest (Dressino, et al., 2004).

An approach that has been eluded within the evolutionary explanations is the one related to the contributions of physiology. Physiology was considered a consequence of evolutionary processes and not a part of them. Anyhow, Noble (2013) stated that the physiological function and the interactions with the environment are factors that influence the speed and nature of inherited changes. Nowadays, several theoretical approaches, supported by empirical evidence, have shown the role of physiological processes as evolutionarily significant extra-genetic adaptation mechanisms. These approaches have also shown the hereditability of some of these physiological processes mediated by, for example, epigenetic processes (Gissis & Jablonka, 2011; Jablonka & Lamb, 1995, 2007, 2014; Negri &

Jablonka, 2016). In this sense, Jablonka & Lamb (1991, 1995) suggested that epigenetic inheritance systems enable the environmentally induced phenotypes to be transmitted between generations. Therefore, these systems have a substantial role during speciation. They argued that divergence of isolated populations may be first triggered by the accumulation of heritable phenotypic differences that are later followed and strengthened by genetic changes. This argument is relevant as an alternative mechanism to speciation. Yet, the real divergence between heritable epigenetic marks diminishes or eliminates the genetic barrier between two adaptive peaks (Pál & Miklós. 1999). Therefore, an epigenetic inheritance system can increase the probability of transition from one adaptive level to another. The authors also stated that peak shift may be initiated by: (i) slight changes in the inducing environment, or by (ii) genetic drift of the genes controlling epigenetic variability. On the other hand, drift-induced transition is facilitated even if phenotypic variation is not heritable. Therefore, Pál & Miklós's thesis is that evolution can proceed through suboptimal phenotypic states, without passing through a deep adaptive valley of the genotype, which affects the dynamics and mode of reproductive isolation.

Another studied mechanism is the action of retrotransposons, which are DNA fragments copied as RNA sequences and inserted in the genome through reverse transcriptase (Noble, 2006, 2008, 2013; Noble, et al, 2014). This mechanism represents an increase in the complexity of the inheritance by making possible the RNA-DNA sense contradicting the DNA-RNA dogma. On the other side, DNA transposons can use a cut and paste mechanism that does not involve an RNA intermediate, as observed in prokaryotes and eukaryotes. According to Beurton, et al. (2000), cellular enzymes are capable of manipulating DNA in order to perform certain functions. In this sense, a genome is composed of semi-stable elements that can be arranged or moved around the genome, thus modifying the information content of DNA. Associated with these approaches, the role of endocrine disruptors has become especially important within the field of extra-genetic adaptation mechanisms. These disruptors are present in the environment as elements which are capable of modifying gene expression and are transmissible over several generations, even when the disruptor is no longer present (Gilbert & Epel, 2009) Thus, Noble (2013) asserted that the "gene" actually is an inherited phenotype, more than an inheritance mechanism.

Another way to address the research and understanding of physiological adaptation is through the modular concept of adaptation (Dressino, 2005). First, it is necessary to understand the criteria that allow for module identification. According to Winther (2001), four basic properties enable module characterization:

1. Modules have differential genetic specifications. Thereby, higher-level modules than the gene are built upon specific genes for that module.

2. Modules are repeated and kept throughout different hierarchical levels and in similar or different contexts.
3. There is a strong connectivity within modules, and a weak one among modules.
4. Modules change and vary over phylogenetic and ontogenetic time.

This characterization applies to different organization levels, from the molecular to the organic one. Moreover, the modular approach to physiological adaptation can be briefly conceptualized as follows.

A physiological module represents an adaptation if it is a compensatory response to an alteration produced by one or more stressors that can maintain or reestablish homeostasis (Dressino, 2005). According to this definition, a stressor or stressing factor refers to external or internal stimuli that trigger reactions that tend to disrupt the organic balance.

Several examples that conform to this definition could be mentioned here. A worth-mentioning example is the "walking hibernation" of polar bears (*Ursus maritimus*), which has been observed in males and non-pregnant females, while pregnant females go into deep hibernation. The extremely cold weather conditions are correlated to scarce food resources. Under the combination of these stressors (cold weather and food shortage), polar bears develop a complex network of physiological adaptations. Polar bears' body temperature in normal conditions is between 37-38 °C, while during hibernation it descends up to 31-36 °C. They also lose a lot of body weight. During hibernation, polar bears recycle the urea in order to produce proteins and avoid blood poisoning. In addition, lipid catabolism significantly increases, together with a decrease in the hypothalamus-pituitary-thyroid axis, which induces a strong hypothyroidism. This reduces the general metabolic activity, only enabling the basic metabolic functions. However, the brain and the heart maintain a temperature similar to one they have during the rest of the year (Folk, et al., 1976; Bruce, et al., 1990; Hellgren, 1998). These physiological features allow us to assert that they comply with the four module characterizations proposed by Winther (2001) as well as with the modular definition of physiological adaptation (Dressino, 2005).

PHENOTYPIC PLASTICITY: A NECESSARY BRIDGE BETWEEN PHYSIOLOGICAL ADAPTATION AND NICHE CONSTRUCTION

The modular structure of adaptation cannot be fully understood if phenotypic plasticity is not considered. In effect, plasticity is an important biological characteristic to understand organism variability in a changing environment. Typically, this variability has been conceptualized as genotype-dependent, that is, genes' differential expression of a genotype to produce different phenotypic variants. This conceptualization of phenotypic plasticity relates to the "reaction norm" concept, which refers to the set of phenotypes that can be produced by an individual genotype. In this sense, plasticity is closely connected to extra-genetic adaptation against environmental changes. As it was previously mentioned, these changes may be of different types: temperature, pH, moisture, nutrition, etc. The phenotypic responses to these changes may be expressed during growth at the morphological or physiological level, among others. Nowadays, research about plasticity has revealed the complexity of the mechanisms that compose it, which are basically translation, transduction, transcription and hormonal regulation that does not strictly depend on the genetic level.

For example, the transcription mechanism is relevant due to the comprehension of the *alternative splicing*, in which all splicing mistakes of mRNA codons act as gene expression multipliers in several proteins, without modifying the protein coding genes, but arranging them in a differential manner (polycistronic RNA that present several codons). In this way, transcription-derived mRNA—in the form of primary RNA transcript or precursor RNA or pre-RNA—is not active but must comply with a series of steps to arrive at the mature form. Therefore, the importance of this mechanism is that not only the expression of a genotype to a specific environment is necessary, but also the "errors" of copying the transcript, thus multiplying phenotypic variability.

Many authors have addressed in detail the adaptation-phenotypic plasticity relationships (Pigliucci, 2001; West-Eberhard, 2003, 2005; Ghalambor et al, 2007; Gilbert & Epel, 2009; Fusco & Minelli, 2010; Day & McLeod, 2018). In general, most authors recognize two basic "plasticity" concepts: "adaptive plasticity" and "non-adaptive plasticity." The first concept must consider the correlation between trait or character plasticity and adequacy among the different environments where it arises. This is why plasticity is adaptive inasmuch as individuals have the reasonable possibility of experimenting alternative environments. For the purposes of this work, the relevance of this plasticity type is that it allows us to understand the colonization of new ecological niches and the rapid divergent evolution. Instead, the second concept—non-adaptive plasticity—represents the response to environmental variations without increasing its adequacy to them, though it may either promote or inhibit genetic differentiation (Fitzpatrick, 2012). In this sense, there are two closely related concepts: phenotypic plasticity and environmental induction. While plasticity is a characteristic of the organism (or its proneness to express different phenotypes in diverse environments), environmental induction represents the influence of environmental action on the organism. Plasticity may manifest itself in a homogeneous population within a homogeneous environment, while environmental induction may occur when the heterogeneous environment generates phenotypic heterogeneity.

The phenotypic plasticity of reproductive traits can be an influencing factor on the evolution of reproductive isolation (second component of ecological speciation). According to Fitzpatrick (2012), this type of reproductive plasticity can cause a selective breeding, yet its influence on the genetic flow ultimately depends on the maintenance of environmental similarities between parents and offspring. This concept is important with regard to niche construction, where the offspring-"inherited" environment has been modified, to a greater or lesser extent, by their parental generation. Therefore, since selective breeding is carried out in a different environment, it would represent an important evolutionary factor. In short, plasticity could be considered an influencing factor on the speciation process (Frankino & Raff, 2004; Schlichting, 2004; West-Eberhard, 2003, 2005).

Recent studies about transgenerational phenotypic plasticity have shown that it is a fast non-genetic response to environmental modifications that can buffer the effects of stresses on populations (Sentis, et al., 2018). The authors monitored the pea aphid (*Acyrthosiphonpisum*) transgenerational phenotypic response to predators, such as ladybirds, during 27 generations of experimental evolution in the absence of initial genetic variation (cloned population starting from a single individual). Results revealed that the frequency of winged aphids first increased rapidly in response to predators and then remained stable over 25 generations. This implies a stable phenotypic reconstruction at each generation. An interesting aspect to mention is that aphids continuously exposed to predators for 22 generations evolved a significantly weaker plastic response than aphids never exposed to predators. The data of this experiment showed the evolution of plasticity in the absence of initial genetic variation and highlighted the importance of integrating several components of non-genetic inheritance to detect evolutionary responses to environmental changes. Moreover, the rhythm of the observed change tendencies may suggest that the gradual changes observed involved the action of reversible epigenetic mechanisms.

NICHE CONSTRUCTION

The "niche construction" concept was originally proposed by Lewontin (1983) by pointing out that organisms do not passively adapt to conditions in their environment, but actively construct and modify environmental conditions and maybe to influence other environmental sources of selection. This idea meant the beginning of new approaches in evolutionary biology as well as in different related disciplines. The 'niche construction' was proposed by John Odling-Smee (1988) asserting that it should be recognized as an evolutionary process. "Niche construction" is a complex concept that is usually very broad and has multiple facets that may lead to some confusion in its use. This problem is partly derived from its link to the concepts of ecological niche, natural selection and adaptation, and from its relevance as an explanatory principle of certain evolutionary processes. The concept is comprehensive since it includes the modification of metabolic activity in relation to cultural changes, such as the modification of eating habits, etc. Bonduriansky & Day (2018) have recently developed the concept of "extended heritage" showing how the mechanisms of non-genetic inheritance (epigenetic, behavioral, environmental and cultural) can play an important role in evolution. On the other hand, the intersections between niche construction and natural selection have generated a strong controversy that remains in force (Laland, et al., 2014).

According to Laland, et al. (2016), the niche construction theory is based upon four tenets: 1) organisms modify environmental states in nonrandom ways, thereby imposing a systematic bias on the selection they generate, and allowing organisms to exert some influence over their own evolution (Odling-Smee, et al., 2003; Laland, 2014); 2) ecological inheritance strongly affects evolutionary dynamics (Odling-Smee, et al., 2013), and contributes to parent-offspring similarity (Danchin, et al., 2011; Bonduriansky, 2012; Badyaev & Uller, 2009); 3) acquired characters and byproducts become evolutionarily significant by affecting selective environments in systematic ways, and 4) the complementarity of organisms and their environments (traditionally described as 'adaptation') can be achieved through evolution by niche construction (Odling-Smee, et al., 2003). Moreover, Matthews, et al. (2014) proposed a set of criteria to test for the presence of niche construction, from which we will only analyze the ones that are relevant to the aims of our research. These are: a) an organism must significantly modify environmental conditions, and b) organism-mediated environmental modifications must influence selection pressures on a recipient organism. These pressures on the recipient organism could be understood by assuming the selective pressures on genotypes. Thus, this last criterion is important for an adaptive niche in an evolutionary sense, in line with a traditional perspective of the modern synthetic theory, and it would not have an impact on extra-genetic adaptations. However, molecular genetics current evidence and the genome sequencing have demonstrated the ambiguities and contradictions of the synthetic theory. This evolutionary perspective is unnecessarily restrictive, nevertheless, the reintroduction of the physiological function and the interactions with the environment are factors that influence the speed and nature of inherited changes. All acquired characteristics can be inherited, and in a few but increasingly more cases, it has been demonstrated that inheritance is robust and intergenerational (Noble, 2013).

On their part, advocates of niche construction perspective assume that it is simply an adaptation. Phenotypes are considered to modify local environments when constructing the niche. In addition, each generation inherits genes and the environment as modified by the ancestral organisms. This relationship between genes and environments from one generation to the next creates a synergy that is transmitted in a modified form. Likewise, the niche construction perspective enables the incorporation of abiotic environmental components and the interactions between biota and abiota in evolutionary models as evolutionary control networks begin to emerge (Odling-Smee, et al., 2003).

An extensive bibliography addresses adaptation from an evolutionary perspective related to natural selection. Even so, extra-genetic adaptation cannot be posited within such framework because it does not depend on natural selection and is the result of each individual's physiological features. Epigenetics comprises a special case, in which the influence of methyl groups over certain genes and histones can be transmitted for several generations, depending on the species. Further, we need to consider that this transmissibility is reversible.

Numerous works show the importance of epigenetic mechanisms in adaptive and evolutionary processes. For example, Weiss, et al. (2016) made some research on *Daphnia* (Cladocera, Crustacea) which revealed the development of defenses against the presence of a predator, such as dipteran larvae *Chaoborus* or its pheromones (kairomones). In turn, there is evidence of postpartum cultural transmission in rats from mothers to their female offspring (Champagne, 2008). This transmission is based on the neuroendocrine system's molecular mediators, where the interactions between estrogen-oxytocin and the differential methylation of estrogen hypothalamic recipients take place. In rats and human beings, the cultural-physiological transmission can be observed in several generations.

The existing complexity between niche construction and extra-genetic adaptation requires complex research and designs; anyhow, the existing data allow us to consider that both concepts are integrated. It is worth recalling that evolutionary niche construction is also related to genetic adaptation. This has been shown in the evolution of the lactase enzyme production in order to split lactose into glucose and galactose in adult human beings, thus favoring livestock development (Cavalli Sforza & Feldman, 1981).

CONCLUSIONS

The line of argument of this work intends to show the relationships between extra-genetic adaptation and niche construction through phenotypic plasticity as an evolutionary factor. In this sense, a first conclusion may be that, given the conceptual interconnection between these terms, it is very difficult to use them independently. Based on the arguments presented, the conjunction of these terms is clearly relevant as possible evolutionary mechanisms. These can be from the role of reproductive plasticity or from the participation of extra-genetic adaptation as a factor in the differential reproductive success. As previously mentioned, epigenetic processes play a role in reproductive isolation, which is the first step towards a possible speciation. Likewise, transgenerational phenotypic plasticity, in the absence of initial genetic variation and with the influence of epigenetic factors, proved to be a potentially relevant evolutionary agent.

As it was previously shown, niche construction is also a concept that involves both aspects of adaptation: genetic and extra-genetic adaptation. In this context, this work may act as a bridge between classical approaches of evolutionary theory and as an alternative perspective based on the reversibility of extra-genetic and physiological inheritance. Due to all the previous arguments, it can be inferred that extra-genetic adaptation and phenotypic plasticity play an essential role in the first stages of a species evolution through niche construction. This evolutionary perspective is not directly related to the gene-centered traditional perspective mediated by natural selection. However, a flexible and even reversible alternative mechanism allows the organism to modify the environment in order to leave an inherited niche to its offspring, different from their parents' one. In the constantly changing organism-environment dynamic, the organism's phenotypic manifestations (e.g. culture) become particularly important as factors of environmental change.

Finally, regarding all previously mentioned debates about whether niche construction may represent an alternative concept to natural selection (Laland, 2014), it is important to consider extra-genetic adaptation, phenotypic plasticity and niche construction as evolutionary mechanisms independent from classical evolutionary approaches, as indicated by several empirical data. Furthermore, these mechanisms should be investigate as an evolutive research programme by its complexity.

ACKNOWLEDGMENT
I want to thank Susana Gisela Lamas for his critical comments. This research was funded by the Universidad Nacional de La Plata through grant 11/N775.

REFERENCES

Badyaev, A.V. & Uller, T. (2009), "Parental effects in ecology and evolution: mechanisms, processes and implications", *Philos Trans R Soc B* 364: 1169–1177.

Bernard, C. (1859/1956), *Introduction à l´étude de la médecine experimental. Introducción al estudio de la medicina experimental*. París: Collège de France / Buenos Aires: El Ateneo.

Beurton, P.J; Falk, R; Rheinberger, H.-J. (2000), *The Concept of the Gene in Development and Evolution: Historical and Epistemological Perspectives*. Cambridge University Press: Cambridge, UK.

Bock, W.J. & Wahlert, G.v. (1965), "Adaptation and the form-function complex", *Evolution* 19(3): 269-299.

Bonduriansky, R. (2012), "Rethinking heredity, again", *Trends Ecol Evol* 27: 330–336.

Bonduriansky, R. & Day, T. (2018) *Extended Heredity: A New Understanding of Inheritance and Evolution.* Princenton: Princenton University Press.

Bruce, D.S.; Darling, N.K.; Seeland, K.J.; Oeltgen, P.R.; Nilekani, S.P.; Amstrup, S.C. (1990), "Is the polar bear (*Ursus maritimus*) a hibernator?: continued studies on opioids and hibernation", *Pharmacology Biochemistry and Behavior* 35 (3): 705-711.

Cannon, W B. (1932), *The Wisdom of the Body*. New York: W W Norton & Co.

Cavalli-Sforza, L.L. & Feldman, M.W. (1981), *Cultural Transmission and Evolution: A Quantitative Approach*. New Jersey: Princeton University Press.

Champagne, F.A. (2008), "Epigenetic mechanisms and the transgenerational effects of maternal care", *Frontiers in Neuroendocrinology* 29: 386–397.

Danchin, E.; Charmantier A.; Champagne F.A.; Mesoudi, A.; Pujol, B.; Blanchet, S. (2011), "Beyond DNA: integrating inclusive inheritance into an extended theory of evolution", *Nat. Rev. Gene.t* 12: 475–486.

Day, T. & McLeod, D.V. (2018), "The role of phenotypic plasticity in moderating evolutionary conflict", *Am. Nat.*, 192 (2): 230-240.

Dressino, V. (2005), "Theoretical and semantic aspects of the modular physiological adaptation", *Rivista di Biologia / Biology Forum* 98: 265-278.

Dressino, V.; Denegri, G.M.; Lamas, S.G. (2004), "Alcances y limitaciones de la definición de adaptación aplicada al fenómeno del parasitismo: una propuesta teórica". *Episteme* 19: 69-80.

Fitzpatrick, B.M. (2012), "Underappreciated consequences of phenotypic plasticity for ecological speciation", *International Journal of Ecology,* article ID 256017,

12 pages. https://doi.org/10.1155/2012/256017.
Folk, G.E. (1966), *Introduction to Environmental Physiology: Environmental Extremes and Mammalian Survival*. Philadelphia: Lea & Febiger.
Folk, G.E.; Larsen, A.; Folk, M.A. (1976), "Physiology of hibernating bears", in Pelton, M.R.; Lentfer, J.W.; Folk G.E. (eds.), *Bears, Their Biology and Management*. Morges, Switzerland: International Union for Conservation of Nature and Natural Resources.
Frankino, W.A., Raff, R.A. (2004), "Evolutionary importance and pattern of phenotypic plasticity: Insights gained from development", in T.J. DeWitt and S.M. Scheiner (Eds.), *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford: Oxford University Press.
Frisancho, A.R. (1996), *Human Adaptation and Accommodation*. Ann Arbor: The University of Michigan Press.
Fusco, G.; Minelli, A. (2010), "Phenotypic plasticity in development and evolution: facts and concepts", *Phil. Trans. R. Soc*. B, 365: 547–556.
Ghalambor, C.K.; McKay, J.K.; Carroll, S.P.; Reznick, D.N. (2007), "Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments", *Functional Ecology* 21(3): 394–407.
Gilbert, S.F.; Epel, D. (2009), *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution*. NY: Sinauer Associates.
Gissis, S.B.; Jablonka, E. (2011), "Transformations of Lamarckism". *Vienna Series in Theoretical Biology*. Cambridge, Mass.: Massachusetts Institute of Technology.
Hellgren, E.C. (1998), "Physiology of hibernation in bears", *Ursus* 10: 467–477.
Jablonka, E. & Lamb, M.J. (1991), "Sex chromosomes and speciation", *Proc. Roy. Soc. Lond*. B 243: 203-208.
Jablonka, E. & Lamb, M.J. (1995), *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*. Oxford: Oxford University Press.
Jablonka, E. & Lamb, M.J. (2007), "The expanded evolutionary synthesis—a response to Godfrey-Smith, Haig, and West-Eberhard", *Biol Philos* 22: 453–472.
Jablonka, E. & Lamb, M.J. (2014), *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*. Cambridge, Massachusetts: MIT Press.
Laland, K.N. (2014), "On evolutionary causes and evolutionary processes", *Behav. Process*. doi:10.10.16/jbeproc201405008.
Laland, K.N.; Uller, T.; Feldman, M.; Sterelny, K.; Müller, G.B.; Moczek, A.; Jablonka, E.; Odling-Smee, J.; Wray, G.A.; Hoekstra, H.E.; Futuyma, D.J.; Lenski, R.E.; Mackay, T.F.C.; Schluter, D.; Strassmann, J.E. (2014), "Does evolutionary theory need a rethink?" *Nature* 514: 161–164.
Laland, K.; Matthews, B.; Feldman, M.W. (2016), "An introduction to niche construction theory", *Evol Ecol*. 30:191–202.
Laland, K. N.; Sterelny, K.; Odling-Smee, J.; Hoppitt, W.; Uller, T. (2011), "Cause and effect in biology revisited: Is Mayr's proximate-ultimate dichotomy still useful?" *Science* 334: 1512-1516.
Lewontin, R.C. (1978), "Adaptation", *Scientific American* 239: 156-169.
Lewontin, R.C. (1983), "Gene, organism and environment", in Bendall (ed.), *Evolution from Molecules to Men*. Cambridge: Cambridge University Press.
Marx, C.H. (1984), "Los procesos de adaptación en biología", en J. Piaget; P.A. Osterrieth; J. Nuttin; F. Bresson; Ch.H. Marx, F. Meyer (eds.), *Los procesos de adaptación*. Nueva Visión. Buenos Aires.
Matthews, B.; De Meester, L.; Jones, C.G.; Ibelings, B.W.; Bouma, T.J.; Nuutinen, V.; Van de Koppel, J.; Odling-Smee, J. (2014), "Under niche construction: an

operational bridge between ecology, evolution and ecosystem science" *Ecol. Monogr.* 84(2): 245–263.

Mayr, E. (1961), "Cause and effect in biology", *Science* 134: 1501-1506.

Metz, F. (1995), "Les origines du concept d'adaptation physiologique", *Revue philosophique* 4: 463-483.

Negri, I. & Jablonka, E. (2016) "Epigenetics as deep intimate dialogue between host and symbionts", *Front. Genet*. 7: 7. http://dx.doi.org/10.3389/fgene.2016.00007.

Noble, D. (2006), *The Music of Life: Biology Beyond the Genome*. Oxford University Press, Oxford, UK.

Noble, D. (2008), "Genes and causation", *Philos. Transact. A. Math. Phys. Eng. Sci.* 366: 3001–3015.

Noble, D. (2013), "Physiology is rocking the foundations of evolutionary biology", *Exp. Physiol.* 98 (8): 1235–1243.

Noble, D.; Jablonka, E.; Joyner, M.J.; Müller, G.B.; Omholt, S.W. (2014), "Evolution evolves: physiology returns to central stage", *J. Physiol.* 592.11: 2237–2244.

Odling-Smee, F.J. (1988), "Niche-constructing phenotypes", in Plotkin, H. C. (Eds.), *The Role of Behavior in Evolution*. Cambridge, Mass.: The MIT Press, pp. 73-132.

Odling-Smee, F. J.; Laland, K.N.; Feldman, M.W. (2003), "Niche construction: The neglected process in evolution", *Monographs in Population Biology* 37.

Odling-Smee, F.J.; Erwin D. H.; Palkovacs E.P.; Feldman, M.W.; Laland, K.N. (2013), "Niche construction theory: a practical guide for ecologists", *Q. Rev. Biol.* 88: 3–28.

Pál, C. & Miklós, I. (1999), "Epigenetic inheritance, genetic assimilation and speciation", *Journal of Theoretical Biology* 200(1): 19-37.

Pigliucci, M. (2001), *Phenotypic Plasticity: Beyond Nature and Nurture*. NY: The Johns Hopkins University Press.

Schlichting, C.D. (2004), "The role of phenotypic plasticity in diversification", in T.J. DeWitt and S.M. Scheiner (Eds.), *Phenotypic Plasticity: Functional and Conceptual Approaches*, Oxford: Oxford University Press, pp. 191–200.

Sentis, A.; Bertram, R.; Dardenne, N.; Ramon-Portugal, F; Espinasse, E.; Louit, I.; Negri, L.; Haeler, E.; Ashkar, T.; Pannetier, T.; Cunningham, J.L.; Grunau, C.; Le Trionnaire, G.; Simon, J-C.; Magro, A.; Pujol, B.; Hemptinne, J-L.; Danchin, E. (2018), "Evolution without standing genetic variation: change in transgenerational plastic response under persistent predation pressure", *Heredity*, https://doi.org/10.1038/s41437-018-0108-8

So, J.K. (1980), "Human biological adaptation to arctic and subarctic zones", *Ann. Rev. Anthropol*. 9: 63-82.

Weiss, L.C.; Heilgenberg, E.; Deussen, L.; Becker, S.M.; Kruppert, S.; Tollrian, R. (2016), "Onset of kairomone sensitivity and the development of inducible morphological defenses in *Daphnia pulex*", *Hydrobiology* 779: 135–145.

West-Eberhard, M. J. (2003), *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

West-Eberhard, MJ. 2005. "Developmental plasticity and the origin of species differences", *Proceedings of the National Academy of Sciences of the United States of America* 102 (1): 6543–6549.

Winther, R.G. (2001), "Varieties of modules: kinds, levels, origins, and behaviors", *Journal of Experimental Zoology (Mol. Dev. Evol.)* 291: 116-129.