



The conceptual structure of evolutionary biology: A framework from phenotypic plasticity

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ABSTRACT

In this review, I approach the role of phenotypic plasticity as a key aspect of the conceptual framework of evolutionary biology. The concept of phenotypic plasticity is related to other relevant concepts of contemporary research in evolutionary biology, such as assimilation, genetic accommodation and canalization, evolutionary robustness, evolvability, evolutionary capacitance and niche construction. Although not always adaptive, phenotypic plasticity can promote the integration of these concepts to represent some of the dynamics of evolution, which can be visualized through the use of a conceptual map. Although the use of conceptual maps is common in areas of knowledge such as psychology and education, their application in evolutionary biology can lead to a better understanding of the processes and conceptual interactions of the complex dynamics of evolution. The conceptual map I present here includes environmental variability and variation, phenotypic plasticity and natural selection as key concepts in evolutionary biology. The evolution of phenotypic plasticity is important to ecology at all levels of organization, from morphological, physiological and behavioral adaptations that influence the distribution and abundance of populations to the structuring of assemblages and communities and the flow of energy through trophic levels. Consequently, phenotypic plasticity is important for maintaining ecological processes and interactions that influence the complexity of biological diversity. In addition, because it is a typical occurrence and manifests itself through environmental variation in conditions and resources, plasticity must be taken into account in the development of management and conservation strategies at local and global levels.

KEYWORDS

Keywords: phenotypic plasticity; conceptual framework; ecology; evolution

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INTRODUCTION

Concepts [“perceived regularity (or pattern) in events or objects, or records of events or objects, designated by label”, Novak & Cañas (2008)] are the media through which theories and scientific communication operate among peers and students. Considering the introduction of new concepts, or discussions about the definitions of relevant concepts, as indicators of scientific progress is not new. Science also progresses when concepts, theories, mechanisms and processes that were not accepted by at least a portion of scientists at the time they were proposed – such as natural selection, genetic assimilation and accommodation, epigenetics and continental drift – are reassessed in light of positive empirical evidence that has accumulated over time.

Consensus among biologists regarding conceptual definitions are, however, relatively rare given that, in biology, several definitions for the same concept is a very common occurrence. This multiplicity of definitions is often the result of each researcher assuming that his or her definition is more ex-

PLICIT than others or that it is context-dependent. On one hand, there seems to be a relatively restricted number of biologists who are concerned with the status of concepts in their science. Consider, for example, the frequency by which phenotypic plasticity appears in the literature (which can be considered a partial measure of the importance that scientists attribute to it), as well as whether the properties of the entities, mechanisms and processes that characterize the phenomena under study are clearly expressed, which, in this case, is phenotypic plasticity (e.g. West-Eberhard 2005; Crispo 2007; Pigliucci 2008; Fusco & Minelli 2010; Scheiner 2010; Forsman 2015). On the other hand, there are those who do not seem to care about this important conceptual aspect of their science, perhaps considering it a concern of philosophy of science. These scientists use concepts as if their meanings are obvious and, perhaps for this reason, seem to assume that they should be understood objectively. This is not the case, however, especially among young scientists, including undergraduate and graduate students,

who may become confused by not clearly understanding the concepts in their area of interest. Ecology, for example, is rich with examples of concepts that are thus treated, such as the concepts of landscape, ecosystem, community and ecological niche (Reiners & Lockwood 2010; Martins 2017), which are difficult to understand because of the complexity of the phenomena they approach and the different contexts to which they refer. The same can be said about the concepts that are recently being used by evolutionists, such as evolvability, robustness, evolutionary capacitance and niche construction (Laland et al. 2000; Pigliucci 2008; Masel & Trotter 2010; Masel 2013).

When concepts of this type are ambiguously or only partially defined their use can be limited by the consequent lack of clarity, resulting in confusion and misunderstanding. This can also promote the accumulation of an indigestible amount of different definitions for the same concept. This is the case for the concept of life, for example, for which there are more than one hundred definitions (Trifonov 2011). This situation can become troublesome because if biologists do not agree on the definition of fundamental concepts, such as the concept of life, the very consistency, rigor, and reliability of biological knowledge, and its adequate disclosure, may be threatened.

Nonetheless, a succinct definition of any concept in evolutionary biology is necessarily limited since the expression of most biological phenomena is dynamic, complex, and subject to variation resulting from accidents and other types of constraints. Consider, for example, the period prior to fertilization and zygote formation (when mating preference occurs), and the period of development (when modules are formed). In addition, conspecific and interspecific interactions that an individual can establish, as well as its relationships with environmental conditions, at different stages of its lifecycle, may

also be subjected to constraints (costs and limits), such as genetic costs and the reliability of cues for phenotypic plasticity (Murren et al. 2015; Scheiner et al. 2017).

Consider, for example, the concept of optimum phenotype used in certain ecological-evolutionary models based on optimization theory. Although this concept has a heuristic value for understanding certain aspects of evolutionary dynamics (e.g. fitness function), the real impossibility of evolving an optimal phenotype (but not an optimal trait) in nature that is inter-generationally predominant in a population must be acknowledged (see Martins et al. 2017). The difference between fitness and quality can be understood in light of the theory of life history, which holds that there is a trade-off between the energy used by organisms to survive and that used to reproduce. Organisms adopt two ecological-evolutionary strategies regarding the use of energy to survive and reproduce, which are the two components of fitness. Those organisms that invest a lot of energy in producing a small number of offspring usually invest in parental care. In contrast, organisms that invest much of their assimilated energy into producing numerous offspring usually do not invest in parental care. This is the difference between fitness and quality: numerous offspring, higher mortality, less quality per individual versus reduced offspring, lower mortality, and higher individual quality in terms of survival probabilities and future reproduction. In reality, each population possesses a variety of phenotypes whose attributes vary qualitatively and quantitatively in time and space, and under the changeable conditions to which it is subjected throughout its area of distribution. Given this reality, both random variation and variability (see Wagner & Altenberg 1996) and environmental variation and variability (especially for phenotypic plasticity) are key concepts that researchers have come up with in the development of knowledge in evolutionary biology and ecology.

Key concepts in evolutionary biology are those that interact with other concepts and play a central and integrative role in understanding evolutionary phenomena. Key concepts, therefore, help to provide a consistent conceptual framework. This integration is important for acquiring a comprehensive view and assessing the degree of advancement of knowledge that a key concept and its interactions with other adjunct concepts can provide to evolutionary biology as it progresses.

On the other hand, there is consensus that there are three main sources of random genetic variation in populations: accumulation of mutations that have adaptive value and, therefore, provide differential survival and reproduction in changing environments; sex that allows the introduction of new recombinations; and gene flow (in opposition to differentiation), which maintains the distribution of populations (Slatkin 1987). However, phenotypic plasticity, when adaptive, can also produce variation that enhances fitness of a population (Price et al. 2003), and thus contribute to expanding its distribution of a given population (Baldwin effect). In addition, the interaction between selection and plasticity can also be adap-

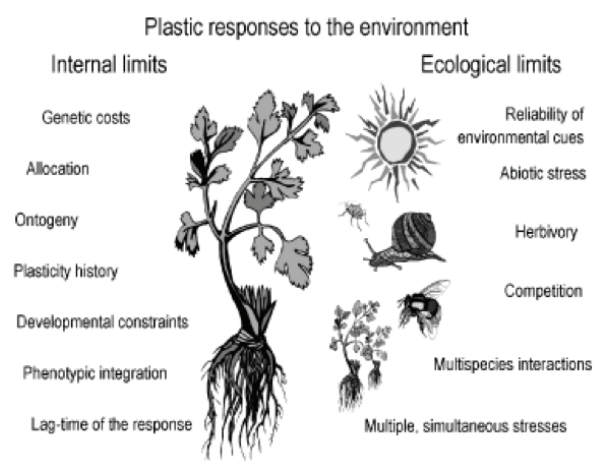


Figure 1. Many internal and ecological factors can influence the capacity of plants to respond to a given environmental factor. While internal limits to plasticity have received sustained attention, ecological constraints and costs induced by multiple biotic and abiotic factors, which more often than not exert their influence simultaneously, have been explored in less detail, despite the growing evidence of their importance (from Valladares et al. 2007).

tive in environments beyond the distribution of a population, and thus contribute to its expansion (Grenier et al. 2016).

Although I agree with Grenier et al. (2016) when, in their review of phenotypic plasticity and adaptation, they claim that the effects of plasticity occurring over the lifetime of individuals can be observed in a single generation, I disagree when they claim that this is not true with the effects of selection. Clearly, the authors consider a definition of selection by which it only works intergenerationally; that is, heritability is a prerequisite (e.g. Endler 1986), which is not entirely correct. The effects of selection agents on phenotypic variation, mainly survival, can also be recorded over the span of a single generation (see Scheiner et al. 2000). Nonetheless, both the process of selection, of course, and phenotypic plasticity, as well as environmental variation and variability, need to be considered key concepts in contemporary evolutionary biology.

1. THE EVOLUTIONARY PACE OF THE DYNAMICS OF PHENOTYPIC PLASTICITY

In addition to environmental variability, environmental variation and natural selection, phenotypic plasticity can also be considered a key integrative concept. Phenotypic plasticity can decrease the response to selection, be it directional, stabilizing, or disruptive. Adaptive plasticity can inhibit evolution by replacing the usual genetic determination. Plasticity can also facilitate evolution by accelerating and directing it because of genetic assimilation and the Baldwin effect (for definitions, see Table 1). In addition, nonadaptive phenotypic plasticity can accelerate (by shifting a trait in the opposite direction of the optimum) or inhibit (by decreasing fertility) evolution, cause phenotypic divergence by generating an immediate response to environmental variation, as in the case of polyphenisms (individuals with identical genomes that respond to environmental variation by expressing different developmental pathways, as in the case of different morphs of water fleas in the absence or presence of predators), and promote speciation by accelerating the development of pre-zygotic isolation mechanisms as in the case of divergent, environmentally triggered, resource-use phenotypes (polyphenisms) within a population (e.g. omnivorous and carnivorous tadpoles; Pfennig et al. 2010; Markov & Ivnitisky 2016).

The evolution of phenotypic plasticity, although not always adaptive (e.g. Palacio-López et al. 2015; Hendry 2016), can also result in local adaptation when new environments are colonized (Baldwin effect). As a result, it can contribute to expanding the range of individual phenotypic variation along gradients of variable environmental conditions (reaction norms) and thus contribute to broadening the area of distribution of the population.

Due to the dynamism that all these characteristics are capable of imparting to evolution (as illustrated by the examples mentioned above), phenotypic plasticity has the potential to integrate other related concepts and processes (the

latter being syntactically and semantically composed of several concepts necessary to characterize its structure and functioning, such as natural selection, for example).

Beyond understanding the role played by selective agents (explicitly ecological) as causes of the process of natural selection (e.g. Wade & Kalisz 1990; Bock 2003; MacColl 2011), there are other concepts—development, modularity, speciation, genetic and phenotypic assimilation, genetic accommodation, Baldwin effect, genetic and environmental canalization, reaction norm, evolvability, robustness, evolutionary capacitance and niche construction—that, to different degrees of magnitude, are related to phenotypic plasticity and can be integrated into a consistent framework through the use of conceptual mapping.

2. IMPORTANCE OF USING THE CONCEPTUAL MAP IN EVOLUTIONARY BIOLOGY

The interrelationships between the concepts mentioned above and the key concepts of environmental variation and variability, natural selection and phenotypic plasticity can be represented by a conceptual map or conceptual diagram: “concept map is a diagram that depicts suggested relationships between concepts” (Novak & Cañas 2008; Figure 2).

Although often used in education, psychology, and computing, as well as by business organizations and collaborative ventures, as far as I know, conceptual maps have not been used to organize and describe the network of interrelationships among concepts that constitute the conceptual framework of evolutionary biology. Although the use of conceptual maps has the potential to lead to better understanding of the interrelationships among concepts in evolutionary biology, it is only a diagram that illustrates the causal interrelationships between the concepts it addresses. Thus, a conceptual map of evolutionary biology can be a simplified diagram, showing only that relationships exist among key concepts or comprehensive processes, without explicitly detailing the interactions that would provide a detailed understanding of evolutionary biology (Figure 3).

Figure 3 shows how Scheiner (1993) depicts the relationships among the effects that environmental and random processes exert on the developmental program, the influences of the developmental program on itself, and the influences that genotype and evolution exert on each other and on the developmental program. In addition, the influence of the developmental program on the phenotype, through environmental influence, is also indicated. Finally, the diagram also shows that the phenotype and the environment have an influence on the natural selection and this, obviously, extends the influence to evolutionary change. Although the heuristic value of Scheiner’s diagram is undeniable, the dynamics of the relationships among these “big” conceptual components of evolutionary biology is quite complex, which may preclude it from being schematized in a very detailed and clear way with all the details

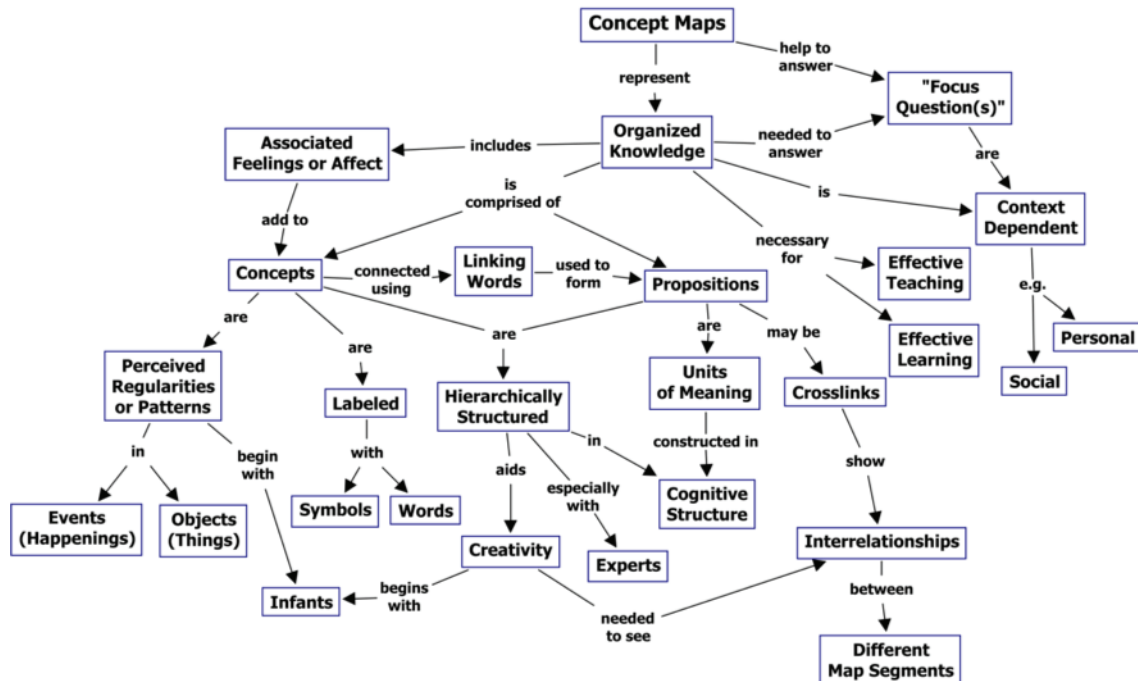


Figure 2. A concept map showing the key features of concept maps. Concept maps tend to be read progressing from the top downward (from Novak & Cañas 2008).

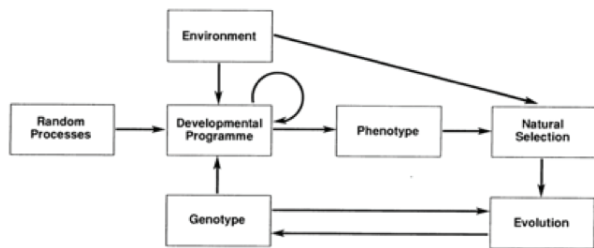


Figure 3. Schematic of the relationships among genetics, development, environment, and evolution. The environment plays a dual role of affecting the developmental process and setting the fitness function. Note that Scheiner's diagram is a simplified one, showing only the relationships between the "big," mainly conceptual, components of evolutionary biology (figure caption modified from Scheiner 1993).

necessary for a comprehensive understanding of evolutionary biology. An alternative, but partial, solution might be to indicate at least part of the complexity involved by approaching the framework of evolutionary biology from certain integrative concepts, such as phenotypic plasticity (Figure 4).

Even when approaching the framework of evolutionary biology in this way — from the perspective of phenotypic plasticity (Fig. 4) — the costs and limitations for the evolution of phenotypic plasticity are not represented and still need to be described in detail, as was the case for the relationships in Fig. 3. Thus, for example, genotype, phenotype and environment, which are obviously focuses of the modern synthesis, can be described by various types of models such as genetic drift, the breeders' equation, adaptive landscapes, and the fitness function. On the other hand, phenotypic plasticity, development, assimilation, accommodation, canalization, robustness, evolu-

ability, evolutionary capacitance, and niche construction are receiving more emphasis, and thus merit attention from the point of view of an integrative theoretical framework of evolutionary biology (Pigliucci 2007; Noble 2015). This integration will need to be further detailed in order to emphasize the dynamics of the relationships that promote it. Therefore, the dynamics of associations among the concepts shown by this conceptual map (Figure 4) need to be described from the perspective of a focal question.

In this study, I present a conceptual map from the perspective of the focal question of the importance of phenotypic plasticity, as well as environmental variation and variability and natural selection, as key concepts for the framework of evolutionary biology. I then use this conceptual map as the basis of a discussion on how and why phenotypic plasticity can play an integrating role for the other concepts mentioned above. First, however, I will address some aspects of the history of the concept of phenotypic plasticity.

3. BRIEF OVERVIEW OF THE HISTORY OF THE CONCEPT OF PHENOTYPIC PLASTICITY

I have not bothered to provide dates for the historical events related to the origin and development of the concept of phenotypic plasticity. Instead I have approached it from the ideas of the main elaborators of concepts and theories, and the proponents of processes, that were explicitly or implicitly based on phenotypic plasticity. Nonetheless, the chronological order of these contributions is maintained. "Natura non facit saltus,"

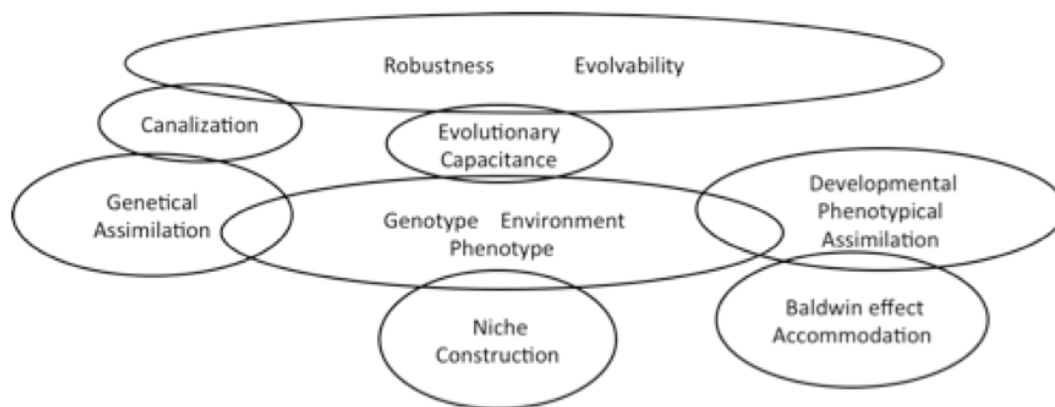


Figure 4. Synthesis diagram of the conceptual interfaces of the mechanisms that influence the evolution of phenotypic plasticity and by which phenotypic plasticity can influence phenotypic evolution. In the center are genotype, environment and phenotype, which mutually interrelate. Environmental stimuli promote changes in genotype (mutations) and phenotype (plasticity). In turn, they both influence the internal (development) and external environment of the phenotype. Below, niche construction influences environmental, genotypic, and phenotypic modifications, thereby interfering with phenotypic evolution. On the right, the Baldwin effect and genetic accommodation can lead to genetic assimilation, which in turn can result in genetic canalization altering the genotype, plastic development of the phenotype, and environment. On the left, genetic assimilation and canalization can promote phenotypic robustness and interfere with evolvability.

says the famous phrase that appears in the writings of Leibnitz as the axiom “la nature ne fait jamais des sauts,” translated into Latin in *Principia Botanica of Linneaus* (wikipedia.org/wiki/Natura_non_facit_saltus). However, a historical account that is intended to be short, such as the present, must necessarily ‘skip’ time intervals and omit some researchers who have reflected on the subject at hand.

The first observations about variation in nature most likely go back to the beginnings of human evolution. Knowing that the intensity of natural selection on certain characteristics can be high (e.g., selection on mating success; Kingsolver et al. 2001; Byars et al. 2010), it is reasonable to suppose, retrospectively, that during the early stages of human evolution — especially those of modern humans — selective agents exerted strong pressures. These selective agents must have favored the evolution of characteristics that resulted in greater relative survival of some individuals over others, and thus greater relative opportunity for them in the early hostile environments in which they existed. If this were otherwise, the original modern human lineage would have gone extinct, since for an individual to survive and reproduce in those hostile environments it would be necessary to discriminate among dangerous, harmless and edible animals, as well as between toxic and comestible plants.

With the evolution of this categorical discrimination, it is likely that child care evolved, in association with, for example, a large brain, reduced sexual dimorphism and complex kinship networks, among other characteristics (see Geary & Flinn 2001). Furthermore, a rapid cultural transmission of discriminatory behaviors, facilitated by the evolution of a large brain, would have gradually increased the probability of survival of those individuals and facilitated the evolution of socialization in structured family groups. There is archeological evidence of human social behavior as early as 40,000 years ago (Mithen 1996). Then, the migration of individuals and the process of local adaptation, favored by the evolution of phenotypic plasticity (Baldwin effect), probably contributed to the relatively rapid

expansion of human populations (circa 200 thousand years ago; Ambrose 1998) in heterogeneous environments throughout the world.

The earliest observations and reflections on variation in nature in the Western thought go back to pre-Socratic philosophers. Heraclitus, for example, realized that everything changes as he watched the flow of a river. He pondered that it would not be possible to drink or bathe in the same water of a river because the water flows continuously. When he said that everything changes, he implicitly refers to environmental variation, or rather, to environmental variability (the potential capacity of the environment to vary).

Although other philosophers, such as Plato, also reflected on variation in nature, especially regarding the continuity or discontinuity of “natural kinds,” Aristotle’s naturalistic realism was largely responsible for deepening the subject among post-Socratics. Aristotle did not believe that biological species were discrete “natural kinds,” but that they presented continuous “variations.” These reflections were the most important precursors for the later development of evolutionary theories (Franklin 1986, and references therein). It was not just this realization that led to Aristotle being considered one of the most prominent naturalists that ever existed: “...he (Aristotle) was and is a great naturalist. When he treats of natural history, his language is our language and his methods and his problems are well-nigh identical with our own” (Romanes 1913). Among the numerous post-Socratic philosophers who reflected on variation in nature, Aristotle was chosen as an example precisely because of his prominence among them, and because addressing the ideas of other philosophers who reflected on variation in nature would not fit this short historical overview.

The most prominent evolutionists who used the concept of phenotypic plasticity (or its equivalent) as a key concept in the development of their theories are showed in the Figure 5.

Lamarck was one of the first evolutionists to recognize the possibility of a direct environmental effect on changes

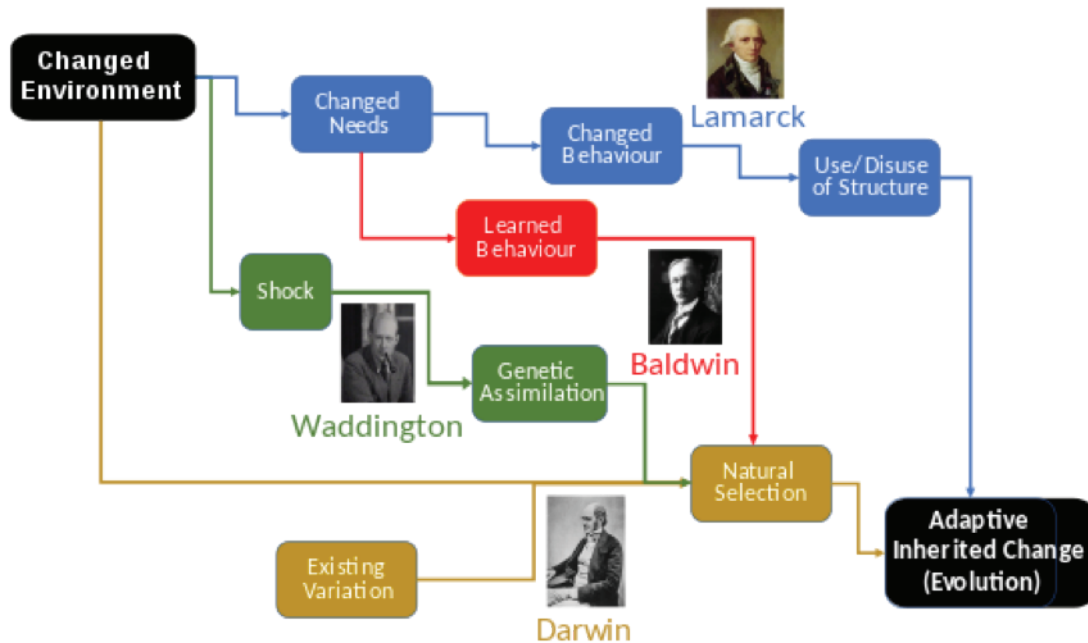


Figure 5. Simplified diagram showing the prominent researchers who used the idea of phenotypic plasticity. Note that other researchers who also made important contributions have been omitted, as explained in the text (figure caption modified from commons.wikimedia.org).

in phenotypic characteristics. However, as is known, his theory of nonhereditary transmission of acquired characters was not accepted among evolutionists: “So far we know this theory is wrong. It is not wrong as a matter of principle, it is an internally consistent and intellectually satisfying theory of evolutionary change. It is wrong as a matter of fact. No mechanism that would act as a specific directing principle to produce appropriate genetic variation has been yet identified” (Bell, 2008).

On the other hand, in terms of principle and fact, Mendelian genetics and the Weismannian conception of the solution of the continuity between the soma and germ, which correspond to the phenotype and genotype, respectively, prevailed (Haig, 2007). However, a type of neo-Lamarckism has revived the idea that acquired characters can be cytoplasmically transmitted (e.g. Shirokawa & Shimada 2016), mainly through the advent of molecular research on the epigenome (epigenetics) and its impact, especially for understanding more than just the origin of genetic diseases (e.g. Bohacek et al. 2018; Feinberg 2018).

Intraspecific variation, as it is now called, was recognized by Darwin as individual variation (Fusco & Minelli, 2010). Although the concept of phenotypic plasticity (*sensu stricto*) was obviously unknown to Darwin, it is very possible that the concept of plasticity was implicit in the term “individual variation” due to the detailed observations that Darwin made on the subject. In addition, since Darwin, the concept of variation has become a key concept in evolutionary biology (Hallgrímsson & Hall 2005).

The importance of the ideas of Waddington and Baldwin is due to their emphasis on the direct effect of the environment on the evolution of adaptive characteristics, in a manner similar to Lamarck with regard to environmental influence. The

famous heat-shock experiment of Waddington (1953), for example, demonstrated how an environmental effect acting on the phenotype during development can be assimilated into the genotype. In turn, Baldwin can be considered the first to develop a theory on the roles played by phenotypic plasticity and learning in allowing the adaptation of organisms to changing environmental conditions during their life span (Scheiner 2014). Nevertheless, despite these earlier effectors, environmentally responsive plastic phenotypes were considered to be of minor relevance because of their supposed lack of a genetic basis (Agrawal 2001). However, Bradshaw (1965) showed the firm genetic basis of phenotypic plasticity: “Plasticity is therefore shown by a genotype when its expression is able to be altered by environmental influences. The change that occurs can be termed the response. Since all changes in the characters of an organism that are not genetic are environmental, plasticity is applicable to all intragenotypic variability.” In this way, Bradshaw contributed decisively to the consideration of phenotypic plasticity in studies conducted under the regency of the modern synthesis (e.g., Scheiner 1993; Scheiner et al. 2000; Scheiner et al. 2017).

As discussed above, biology is replete with concepts that contain vague and imprecise definitions. The history of the concept of phenotypic plasticity reveals that this concept is no exception and has produced its share of controversies. Such issues included whether plasticity itself or plastic traits are the subject of natural selection (see Nicoglou 2015 for a detailed history of the concept in evolutionary biology).

In addition to Baldwin and Waddington, Schmalhausen and Goldsmith were also important researchers who addressed phenotypic plasticity. These four important contributors of precursors to modern developmental evolution-

ary biology (phenotypic plasticity and epigenetics) captured in their studies the concepts of phenotypic plasticity, epigenetic landscape, assimilation and canalization with regard to development (Pfennig et al. 2010; Noble 2015).

Therefore, the recognition that environmental variation directly influences phenotypic change, and that the phenotype is a result of the same genotype interacting along a gradient of variable environmental conditions producing different phenotypes and their respective reaction norms, is the fundamental tenet of the history of the concept of phenotypic plasticity, as far as modern evolutionary biology is concerned.

Although this phenomenon has been recognized more recently by evolutionary biologists (e.g. Weismann, Goldschmidt, Schmalhausen, and Waddington; Pfennig et al. 2010), for over 200 years (Figure 5) the focus of most early evolutionary geneticists on understanding the genetic adaptations of organisms in stable and unstable environments delayed, for some decades, an understanding of the role of phenotypic plasticity in the evolution and diversification of organisms. Emphasis on the importance of phenotypic plasticity began to be addressed in the literature in the 1950s; however, until 1983, about 20 years after Bradshaw (1965), less than 10 works on phenotypic plasticity were published annually. The situation then changed rapidly, with 11,822 papers being published from 1967 to 2013, of which 1,000 were reviews (Forsman 2015).

Therefore, evidence has recently accumulated showing that phenotypic plasticity (adaptive, nonadaptive, and neutral) can be an important mechanism driving organic evolution (e.g. Whitman & Agrawal 2009; Forsman 2015; Palacio-López et al. 2015; Hendry 2016). To some extent, and linked to the recognition of the action of this mechanism, the question arose as to how quickly phenotypic plasticity could produce adaptive responses.

Evolutionary adaptive responses generally occur faster, in ecological time, by phenotypic plasticity. Despite the fact that ecology and evolution might occur on similar temporal scales, changes in population abundances occur faster than changes in traits (DeLong et al. 2016). DeLong et al. (2016) also suggested that slower rates of change for phenotypic traits, compared to population abundances, may be due to high proportions of heritable variation or shallow relative fitness gradients, or, in some cases, a lack of plasticity. Since responses of plasticity should, in general, be faster than genetic changes, it is possible that slower rates of plastic trait change could be more typical of populations in stable rather than in variable or stressful environments (see Ghalambor et al. 2007).

Adaptive phenotypic plasticity is now known to be widespread in nature (Price et al. 2003; Miner et al. 2005). However, in contrast to this observation, Scheiner (2018) argues that adaptive trait plasticity is uncommon, probably due to constraints that the evolution of plasticity experiences from the existence of costs and limitations, even though there is little evidence of costs, unlike constraints. Nonetheless, in spite of Scheiner's statement, and genetic evolution, both in nature and experimentally, and the diversity of ways it can

be expressed, there remain uninhabited places, probably due to high costs and limits to the evolution of plasticity in those sites. These places are very adverse to population growth and persistence, and include extremely hot and cold places in the world. Some exceptions are extremophiles (species that thrive in physically or geochemically extreme conditions that are detrimental to most life on Earth), which are able to tolerate some extreme conditions of temperature and the detrimental effects of other physicochemical factors (Rampelotto 2013). Extremophiles, for instance, evolved adaptive phenotypically plastic traits (e.g. heat-shock proteins that protect against denaturation from high temperature extremes) that enhance the likelihood of surviving and reproducing in extremely hot sites (Chevin & Hoffmann 2017).

Albeit widespread in nature, phenotypic plasticity is never supreme. For instance, in a meta-analysis of 362 records of morphological, physiological, and life history modifications in plants, Palacio-López et al. (2015) found that of all the characters considered 52% were nonplastic. Among the 48% that exhibited some plasticity, 49.4% showed perfect adaptive plasticity, 19.5% phenotypic plasticity, and 31% nonadaptive plasticity. These findings obviously indicate that during the process of phenotypic modification, there are ecological and evolutionary restrictions to the evolution of phenotypic plasticity (see Valladares et al. 2007; DeWitt et al. 1998; Murren et al. 2015; Hendry 2016).

Hendry (2016) presented eight conclusions about the role of phenotypic plasticity in eco-evolutionary dynamics including the costs and limits of plasticity: "(1) Plasticity is—not surprisingly—sometimes adaptive, sometimes maladaptive, and sometimes neutral. (2) Plasticity has costs and limits but these constraints are highly variable, often weak, and hard to detect. (3) Variable environments favor the evolution of increased trait plasticity, which can then buffer fitness/performance (i.e. tolerance). (4) Plasticity sometimes aids colonization of new environments (Baldwin effect) and responses to *in situ* environmental change. However, plastic responses are not always necessary or sufficient in these contexts. (5) Plasticity will sometimes promote and sometimes constrain genetic evolution. (6) Plasticity will sometimes help and sometimes hinder ecological speciation but, at present, empirical tests are limited. (7) Plasticity can show considerable evolutionary change in contemporary time, although the rates of the evolution of this reaction norm are highly variable among taxa and traits. (8) Plasticity appears to have considerable influences on ecological dynamics at the community and ecosystem levels, although many more studies are needed" (Figure 6).

The scarcity of studies on the influence of phenotypic plasticity on community and ecosystem levels makes it difficult to understand the evolution of community structure and organization (Whitman & Agrawal 2009). Since phenotypic plasticity can influence the colonization of new environments, the geographic expansion of populations and speciation, its influence must also be considered a potential factor in the relationship between regional and local diversity. It is also difficult to

Table 1: Definitions of the main concepts that integrate the conceptual framework of evolutionary biology from the perspective of phenotypic plasticity. The criterion for choosing definitions for the concepts related to phenotypic plasticity was based on the author's understanding of the adequacy and clarity that the definitions express. In addition, the authors selected were those who somehow showed relationships among some concepts (details in the text).

Concepts and Processes	Definitions	Authors
Environmental variability	Potential capacity of the environment to vary.	The author of this text
Predictable environmental variation	Predictable temporal and spatial differences in environmental conditions and resources.	The author of this text
Phenotypic plasticity	The capacity of a genotype to produce variable trait states as a function of environmental inputs.	Samuel Scheiner (pers. comm.)
Cost of plasticity	A factor that decreases the fitness of an individual even when the trait matches the optimum.	Scheiner et al. 2017
Limit to plasticity	A factor that prevents an individual from matching the optimum.	Scheiner et al. 2017
Reaction norm	Phenotype produced by an organism that varies as a continuous function of an environmental signal.	Stearns 1989
Evolvability	The ability of biological systems to evolve.	Pigliucci 2008
Modularity	A genotype–phenotype map in which there are few pleiotropic effects among characters serving different functions, with pleiotropic effects falling mainly among characters that are part of a single functional complex.	Wagner & Altenberg 1996
Evolutionary capacitance	Accumulation of hidden genetic variation that may be unleashed under conditions of stress.	Pigliucci 2007
Robustness	Robustness can only be defined unambiguously as the average effect of a particular perturbation on a particular phenotype, relative to some control.	Masel & Trotter 2010
Speciation	The mechanism by which, through anagenesis, a lineage can differentiate into two distinct species by the action of selection, or by cladogenesis in two other species by the action of species selection.	The author of this text
Phenotypic flexibility	The overall ability of an organism to maintain high fitness in different environmental conditions (sensu Bradshaw, 1965).	Samuel Scheiner (pers. comm.)
Developmental plasticity	Irreversible phenotypic variation in traits of individuals (or genotypes) that result from environmentally induced modifications of development and growth.	Forsman 2015
Phenotypic accommodation	Adaptive adjustment of aspects of an organism, which may occur during development without genetic change of variable aspects of the phenotype following a novel input during development.	West-Eberhard 2005
Genetic accommodation	When there occurs both an increase in evolution of plasticity and an increase in genetic canalization (genetic assimilation that is an extreme form of accommodation). The same as environmental canalization (Waddington, 1953)	Ehrenreich & Pfennig 2015
Baldwin effect	Environment-induced change of the phenotype. Same as accommodation.	Crispo 2007
Genetic assimilation	A characteristic fixed in the phenotype that does not manifest plasticity (the same as environmental canalization).	Waddington 1953
Genetic canalization	The complete loss of phenotypic plasticity. Increased canalization is an extreme form of genetic accommodation known as genetic assimilation.	Waddington 1942
Environmental canalization	The same as autonomous development and genetic canalization.	Stearns 1989
Niche construction	The activities, choices, and metabolic processes of organisms through which they define, choose, modify, and partly create their own niches.	Laland et al. 2000

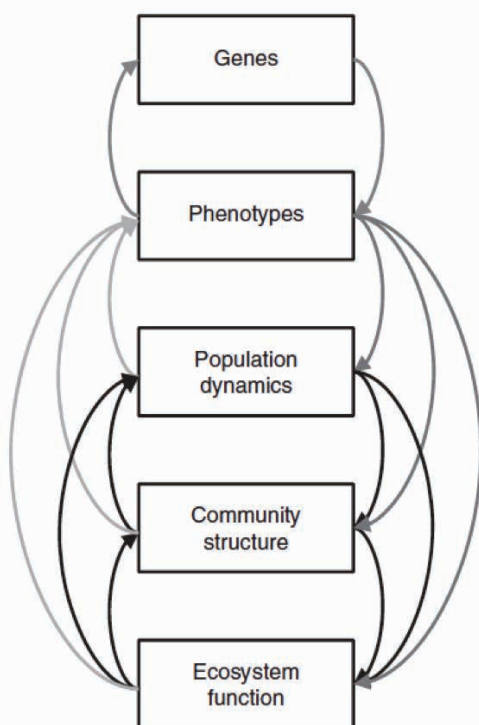


Figure 6. Conceptual diagram outlining the basic elements of eco-evolutionary dynamics outlined by Hendry (2016). Phenotypic traits in a focal species can influence the population dynamics of that species, which can then influence the structure of the community in which that species was embedded, as well as the functioning of the overall ecosystem. In addition, phenotypic traits in the focal species can directly (i.e. not through population dynamics) influence community structure and ecosystem function. Ecological effects at the population, community, and ecosystem levels can then feedback through plasticity or selection to influence phenotypic traits. These phenotypic changes will be passed on to the next generation to the extent that they are heritable. Figure kindly transferred by Andrew Hendry. Figure caption modified from Hendry (2016).

understand the functioning of ecosystems without considering phenotypic plasticity (Hendry 2016; Jackrel & Morton 2018).

4. CONCEPTUAL MAP OF THE RELATIONSHIPS BETWEEN PHENOTYPIC PLASTICITY AND OTHER RELEVANT CONCEPTS OF EVOLUTIONARY BIOLOGY

The definitions, and their authors (Table 1), of concepts whose dynamic interrelationships are depicted in the conceptual map (Fig. 7), were chosen in view of their clarity and relationships established with other such concepts in the same paper by a certain author, or are those elaborated by the author of the present work. In the former case, since the purpose of the present study is to indicate and discuss the dynamic relationships among concepts, preference is given to authors who already indicate at least part of this dynamic interaction. In the latter case, an attempt is made to make the meaning of concepts more comprehensive and clear, considering that I did not find a definition that I thought was more satisfactory. However, I make clear that my concept map is just one of several possibilities. I believe that every evolutionist interested in the

subject would be able to add, replace, or remove concepts and definitions and thus diagram their own conceptual map, but obviously keep the key concepts that characterize the core of this conceptual framework (oval boxes, Fig. 7).

Despite constraints that hinder the evolution of adaptive phenotypic characteristics (e.g. DeWitt et al. 1998; Murren et al. 2015; Palacio-López et al. 2015; Hendry 2016), and considering that individuals and populations have the potential to vary (variability) because of the flexibility with which genotypes and phenotypes (e.g. Piersma & Drent 2003; Fischer 2016) respond to environmental stimuli, it is not unexpected to find individual and population phenotypic variation.

Although the action of environmental selective agents on the genetic variation of random origin expressed by individuals and lineages is obviously the main propeller of adaptive evolutionary changes, in addition to random and deterministic modification in population gene frequencies, environmental stimuli can also directly cause phenotypic changes that modify the expression of certain genes and result in evolutionary adaptations that can be assimilated and canalized into the genotype. These canalized adaptations can lead to genetic robustness, which in turn can enhance evolvability (Masel 2013). In order to avoid confusion between the meanings of genetic assimilation and genetic accommodation common in the literature, Crispo (2007) aptly proposed that the former refers to evidence that shows an adaptive decline of plasticity, whereas the latter refers to any type of change in the reaction norm after exposure to a new environmental stimulus (Fig. 7). Lande's (2009) model of evolution of reaction norms following a sudden change in an average environment predicts that minimum genetic and phenotypic variances should occur if the curvature (breeding value) and slope (plasticity) of the reaction norms are uncorrelated. In the Lande's model, there is no cost or limitation to plasticity evolution. Besides, in that model, prior to sudden environmental change, there is temporal variation that selects for a limited amount of plasticity; when the sudden environmental change happens the temporal variation continues, but after a rise in plasticity it returns to the initial amount because the nonplastic part of the genome achieves with the sudden change. On the other hand, in the Scheiner et al.'s (2017) model of plasticity evolution, except for the sudden change there is no temporal variation: the plasticity increases and stays high following the sudden change, except if there is some cost or limitation selecting against plasticity.

Phenotypic plasticity may play a fundamental role in speciation (Pfennig et al. 2010), and due to its influence on development, which also influences evolvability, it can also affect the propensity for speciation as well as reaction norm evolution (Pigliucci 2008). Finally, niche construction (Laland et al. 2000) leads to natural selection through the action of selective agents and vice versa; that is, natural selection can enhance niche construction. Although the widespread acceptance that genetic assimilation (*sensu* Waddington 1953) may constitute an important effect of the evolution of trait plasticity, it is unlikely that the plasticity of a trait can be replaced by fixed ge-

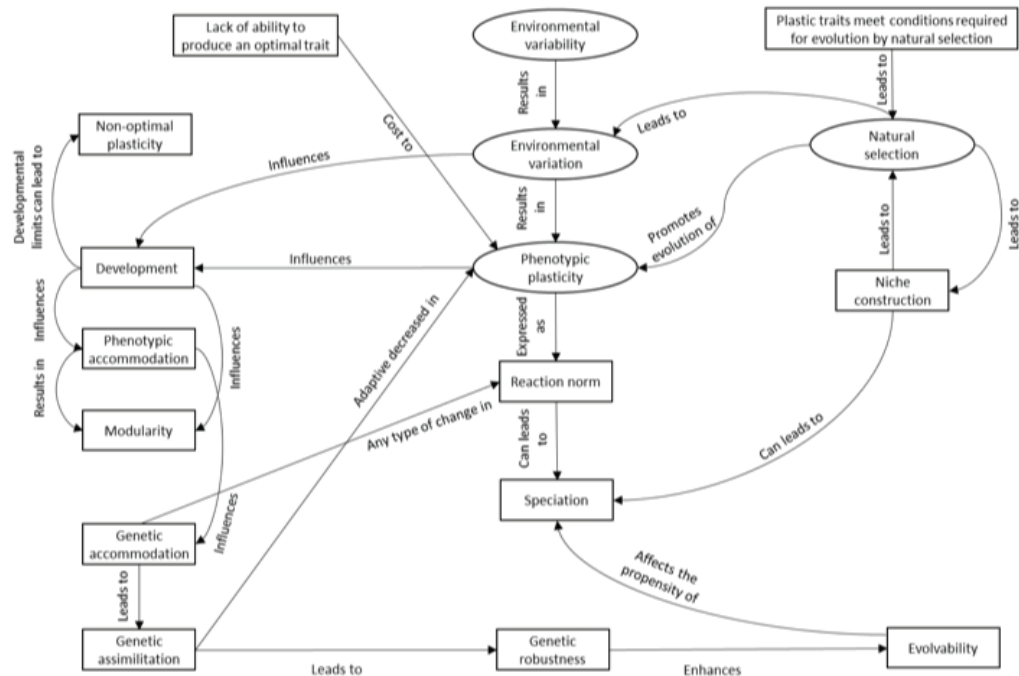


Figure 7. Oval boxes contain the key concepts to which the other concepts (rectangular boxes) of the partial structure of the conceptual framework of evolutionary biology are related dynamically. The benefits, costs, and limitations of the evolution of plasticity are represented in the conceptual map by the way of example so as not to compromise the clarity of relationships because the introduction of all possible benefits, costs, and limitations would result in an agglomeration of concepts that could make it difficult to understand the map (see text for details).

netic effects. The model of Scheiner et al. (2017) predicts that assimilation manifests if the selective environment is stable, or at least that new costs of plasticity manifest themselves after environmental change. Therefore, due to the results of Scheiner et al. (2017), the possibilities for the evolution of assimilation, as described in the conceptual map (Fig. 7), should take into account that this would occur only in circumstances that are likely not as frequent in nature as the broad acceptance of evolution assimilation may make one believe. Scheiner et al. (2017) also add that to demonstrate that assimilation does in fact occur in nature, it would be necessary to evidence that a plastic trait is transient and that the decline of plasticity occurs more due to a cost or limitation of plasticity than due to the influence of other selective factors.

I was “challenged” to include in my conceptual map four statements about the conditions necessary for adaptive evolution of phenotypic plasticity to occur, and three other statements about the conditions (constraints) that would limit the occurrence of such an evolution:

- 1) Existing environmental heterogeneity that affects the phenotypic expression of traits.
- 2) The optimal phenotypic value of the plastic traits varies in space and/or time.
- 3) Individuals or lineages must experience the environmental heterogeneity either within or across generations.
- 4) These plastic traits meet the conditions required for evolution by natural selection.
- 5) Nonoptimal plasticity may result from maintenance, pro-

duction, or information acquisition costs of plasticity.

- 6) Nonoptimal plasticity may result because the environment, at the time that the phenotype is determined, does not provide a reliable cue about the environment at the time of selection.
- 7) Nonoptimal plasticity may result from developmental limitations to plasticity (Samuel Scheiner pers. comm. ; Scheiner 2013).

The first condition is expressed over the definition of the concept of “environmental variability” (Table 1) due to the fact that environmental heterogeneity in time and space results in environmental variability and variation whose influence on phenotypic traits results in variable phenotypic plasticity. Since the optimal values of these traits vary in space and time, if they encounter the necessary conditions for evolution through natural selection, it is possible that the action of selective agents would result in phenotypic flexibility, that is, “the overall ability of an organism to maintain high fitness in different environmental conditions” (Table 1). The third and fourth conditions are necessary for phenotypic plasticity to continue to evolve in the long term in response to temporal and spatial changes in environmental variability.

The other three conditions limiting the evolution of phenotypic plasticity and affecting evolutionary dynamics, the genetic and environmental costs imposed on its evolution, have already been partially discussed above. However, it should be emphasized here that there are at least five poten-

tial costs to phenotypic plasticity and four limits to its evolution (DeWitt et al. 1998): (1) energetic costs of the maintenance of structures; (2) the production costs that plastic genotypes pay; (3) costs of the acquisition of environmental information; (4) phenotype imprecision caused by developmental instability, which can reduce fitness; and (5) genetic costs caused by linkage, pleiotropy, and epistasis; (6) limits to information readability—the production of maladaptive phenotypes by plastic organisms when they are wrong about environment; (7) limits due to lag-time—a time lag between environmental change and a phenotype response can reduce fitness; (8) limits to developmental range—fixed development may be more capable of producing extreme adaptive phenotypes than facultative development; and (9) problems with the epiphenotype—plastic add-on phenotypes may be ineffective compared with the same phenotypic element that is integrated during early development. The main causes that facilitate the evolution of nonoptimal plasticity result, therefore, from the costs and limitations that impose fitness losses (DeWitt et al. 1998; Murren et al. 2015). Note that in Figure 7 only one cost and another example of limitation to the evolution of plasticity were provided, as well as a benefit that can lead to the evolution of plasticity through natural selection (nonoptimal plasticity, limitations of development, and plastic traits meet the conditions required for evolution by natural selection) as representatives of the costs, limits and benefits discussed above, in order to avoid cluttering the concepts and interfering in the ability to understand the interrelationships shown in the conceptual map.

An important distinction to be considered in studies on the adaptability of phenotypic plasticity is that, unlike genetic adaptation, which is intergenerational (adaptation produced by natural selection on genetically heritable variation), adaptive phenotypic plasticity is intragenerational; that is, responses to environmental variation occur in real time (Whitman & Agrawal 2009). Therefore, when adaptive, phenotypic plasticity generally results in faster phenotypic changes than genetic responses (e.g. Scoville & Pfender 2010). However, multivoltine species may exhibit phenotypic plasticity over generations when two or more different phenotypes are repeated in successive generations (Fusco & Minelli 2010).

5. CONCLUDING REMARKS

The use of conceptual maps to illustrate the interrelationships among concepts, mechanisms, and processes that form the

conceptual framework of evolutionary biology is not a typical approach. However, the present work illustrates how the use of a conceptual map can help to understand the structure and organization of the conceptual framework of evolutionary biology. Through the use of a conceptual map it is possible to understand the dynamic interrelationships involved in the rhythm of evolution and, in this specific case, of phenotypic plasticity. When adaptive, plasticity influences, and is influenced by, several mechanisms and processes, as shown by the map. However, although plasticity is not always adaptive, because of the costs and limitations imposed on its evolution in terms of fitness loss, there remains a lot of evidence attesting to its importance for the evolution of the diversity of life.

Ecology and evolution are two interdependent processes. The main mechanism of phenotypic evolutionary change is natural selection, which is mainly the result of interactions, i.e., ecology. For example, mutualists, facilitators, competitors, predators, and parasites interact with each other and determine the evolution of community structure. The evolution of ecological interactions also results in increased diversity and complexity by increasing the likelihood of energy transfer through trophic levels. An expressive number of morphological, physiological, and behavioral characteristics in animals and plants can be adaptive in changing environments. The evolution of ecotypes (phenotypes directly differentiated by environmental variation) may contribute to expanding the distribution area of a population without genetic change occurring.

Since phenotypic plasticity is expressed through direct environmental influence during individual development, its occurrence should be considered important in the structuring and organization of ecological communities and landscapes, and the dynamics of the ecosystem processes of energy transfer and nutrient cycling. From this approach, the importance of phenotypic plasticity to the management and conservation of populations interactions, and ecological processes can clearly be deduced.

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