**The effect of phenotypic plasticity on rates of adaptive evolution in different climatic and phenotypic contexts – patterns and mechanisms**

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**PAPER 1 (CHAPTER 1):**

**The effect of phenotypic plasticity on rates of adaptive evolution in different climatic and phenotypic contexts – mechanisms**

**Abstract**

A plasticidade fenotípica pode afetar a evolução adaptativa tanto pela dificuldade como pela facilitação da evolução genética. Este tema permanece não resolvido devido a pouca compreensão do mecanismo e da associação da mesma com padrões de biodiversidade atuais e futuros – maior compreensão aumentará a previsão sobre os ambientes futuros, inclusive os afetados por seres humanos. Neste trabalho, verificaremos o efeito da plasticidade fenotípica na adaptação evolutiva em diferentes contextos – espera-se que a plasticidade fenotípica facilite a evolução através do aumento das taxas de evolução do traço, de especiação e de extinção. Para tanto, utilizaremos modelagem computacional baseado em agentes (capítulo I – resultados teóricos) e banco de dados de plasticidade fenotípica (capítulo II – confirmação empírica). Na parte teórica, utilizaremos um pacote disponibilizado recentemente no R (gen3sis), no qual facilita responder questões eco-macroevolutivas. Na parte empírica, utilizaremos uma base de dados da Nature, que disponibiliza valores de plasticidade desenvolvimental termal em répteis, no qual servirá para verificar múltiplos estados de especiação e extinção (MuSSE) através de análises filogenéticas no R. Com isso, esperamos que nosso trabalho auxilie no entendimento dos padrões e mecanismos associados a este tema em contextos distintos, fazendo a literatura científica avançar com o surgimento de previsões e pesquisas a partir deste trabalho.

**Keywords:** Anthropogenic changes; climate changes; contemporary adaptation; extended evolutionary synthesis; macroecology; natural selection

**Introduction**

Phenotypic plasticity is the ability of a given genotype to produce different phenotypes in response to distinct environmental conditions (Piglucci 2001). Traditional adaptation models did not include phenotypic plasticity as something important for the future adaptation of species. Nevertheless, this fact has recently changed and, more and more, there is acknowledge of the potential of plasticity in altering the selective and adaptive process of the trait (Ghalambor et al. 2015; Wong e Candolin 2015; Fox et al. 2019). However, it is not clear yet how phenotypic plasticity affects adaptive evolution (Dingemanse and Wolf 2013; Lowry et al. 2013; Wong and Candolin 2015; Kelly 2019; Fox et al. 2019), with evidences indicating that it can as difficult as facilitate genetic evolution (Ghalambor et al. 2007; Wong and Candolin 2015).

Phenotypic plasticity can difficult the adaptation by domination of a phenotype in the population genetic pool, decreasing genetic variation and selecting continuously this plastic genotype that produces the dominant adaptive phenotype (stabilizing selection) (Ghalambor et al. 2007; Wong and Candolin 2015). This domain decreases the directionality of selection and hides the underlying genetic variation, acting as a shield that hinder other adaptive phenotypes for that environment from being selected (Ghalambor et al. 2007; Wong and Candolin 2015). Otherwise, plasticity can facilitate adaptation through canalization (by genetic accommodation or assimilation) of a phenotype of optimal fitness (Ghalambor et al. 2015). This phenotype would decrease the population decline, allowing more time for: (a) genetic changes accumulate (possibility of new beneficial mutations); and (b) selection can act on new phenotypes (directional selection) (Ghalambor et al. 2007; Ghalambor et al. 2010; Wong and Candolin 2015). In this sense, plasticity would be the first step of adaptive evolution and it would alter the selective regime (rate and direction of evolution) (Ghalambor et al. 2015).

Although there are generic explanations for the understanding of how phenotypic plasticity affects adaptive evolution (facilitate or difficult), this theme remains unresolved (Kelly 2019) and it is a controversial problem (Ghalambor et al. 2015). One of the main reasons for this is the little understanding of the mechanism behind this theme and its association with current and future biodiversity patterns (Wong e Candolin 2015; Fox et al. 2019). The difficult in understanding the effect of plasticity on adaptive evolution is related to three main topics: (i) trait evolution (how it occurs, how long it lasts facilitating or making it difficult, in case of the latter, what would be the limit of hinder of plasticity for adaptation) (Wong e Candolin 2015); (ii) macroevolution (time in which it occurs and dynamic of selection of new phenotypes in case of facilitation) (Bro-Jorgensen et al. 2019; Fox et al. 2019); and (iii) the extinctions that arise during the process (Wong e Candolin 2015; Bro-Jorgensen et al. 2019; Fox et al. 2019). Studying this theme and solving problems is considered by Sih (et al. 2011) one of the great contributions that ecology and evolution can offer to the modern world, since in addition to being crucial knowledge for predicting the fate of species in the short and long term, it can help in the future to prevent and combat biodiversity loss (Ghalambor et al. 2010; Ghalambor et al. 2015; Wong e Candolin 2015; Bro-Jorgensen et al. 2019).

Due to the potential that the understanding of the theme has to increase the prediction about future environments, including those affected by human-induced rapid environmental changes (HIREC) (Bro-Jorgensen et al. 2019), it has been suggested that plasticity may affect adaptive evolution of distinct ways in different contexts (Ghalambor et al. 2015; Wong e Candolin 2015; Fox et al. 2019). Some relevant contexts are: (i) type of plasticity – activational (phenotype variation in response to present stimuli – reversible) and developmental (phenotype variation in response to past stimuli – irreversible) (Botero et al. 2014; Stamps 2016; Fox et al. 2019); (ii) behavioral (instinctive and learned) and morphological (ontogenetic) phenotype (Wong e Candolin 2015; Fox et al. 2019); and (iii) disturbance speed (Wong e Candolin 2015; Kelly 2019). It is suggested that in context of rapid climate changes there is a need for rapid adaptation of species (Fox et al. 2019; Kelly 2019). This adaptation, which by the traditional evolutionary model would not occur, due the phenotypes of individuals being plastics, may occur at a relevant time scale to the paceof the environmental changes, thus preventing the extinction of species (Fox et al. 2019; Kelly 2019).

It is expected that, in the distinct scenarios, there will be different adaptive evolution times, being important to define, what types of plasticity will facilitate (if they facilitate) the adaptation in a relevant time scale (Fox et al. 2019). It is expected that: (i) in scenarios of slow climate changes any type of plasticity will facilitate adaptation in an relevant time scale (Botero et al. 2014; Fox et al. 2019); and (ii) in scenarios of rapid climate changes the adaptive facilitation will only occur in relevant time scale in the context of activational plasticity (due to the immediate flexibility of the phenotype) (Botero et al. 2014; Fox et al. 2019).

In this paper, we have 4 chapters – 2 of theoretical modeling (chapters I and III) and 2 of empirical approaches (chapters II and IV – these will serve to confirm the predictions of the models). So, given the context established above, the goal of this project is to understand:

Chapter I – Theoretical modeling and mechanism I. Effect of phenotypic plasticity on adaptive evolution

We expect that phenotypic plasticity facilitates adaptive evolution by canalization the plastic phenotype and selecting other phenotypes.

1. Effect of phenotypic plasticity on evolution rates of the trait

* We expect that plasticity will increase evolution rates of the trait

1. Effect of phenotypic plasticity on speciation rates

* We expect that plasticity will increase the speciation rates

1. Effect of phenotypic plasticity on extinction rates

- We expect that plasticity will decrease extinction rates

Chapter II – Empirical and pattern approach I. Effect of phenotypic plasticity on adaptive evolution

We expect that the results of this chapter, obtained through empirical data, confirm the results that we found in the theoretical model elaborated in chapter I.

Chapter III – Theoretical modeling and mechanism II. Effect of phenotypic plasticity on adaptive evolution in different contexts

All contexts will facilitate adaptive evolution, however in distinct speeds.

(a, b and c) Effect of phenotypic plasticity on evolution rates in disturbance of low and fast speed.

- We expect that phenotypic plasticity will increase evolution rates of the trait, speciation rate and decrease the extinction rate independent of disturbance speed. This effect will occur more quickly in cases of activational than developmental plasticity, given that this first is a quick response and it does not depend on alternating generations – the plastic genotype will be selected, dominate the genetic pool and will be canalized faster, being useful mainly for the adaptive selection in the context of rapid disturbances as habitat loss. Genotypes that are plastic in development tend to go for the ideal phenotype (“tendentious” selection), the delay in the selective process is basically due to the fact that it occurs between generations – it will serve more for slow disturbances. The same expectation that we have for activational plasticity, we have for behavioral phenotypes – for the same reasons already mentioned, beyond of flexibility that it has in comparison with morphological phenotypes.

Chapter IV – Empirical and pattern approach II. Effect of phenotypic plasticity on adaptive evolution in different contexts

We expect that the results of this chapter, obtained through empirical data, confirm the results that we found in theoretical model elaborated in chapter III.

**Material and methods**

Characterization

In this chapter, we will search to understand the mechanisms behind how phenotypic plasticity affects adaptive evolution. We will do this through computational modeling – recommended (Botero et al. 2014; Ghalambor et al. 2015) approach to understand mechanisms and systems with great complexity, due the fact that we can control the parameters to test different combinations of them.

*MODEL*

We will elaborate a 100x100 world with 20 species, being that each one them will have an initial population of 100 individuals each – they will have the same life span. Although there are many concepts of species spread in the literature applied to different biological contexts (Queiroz 2007), in our work we will adopt the concept of Mayr (1963): clusters of intercrossing natural populations, reproductively isolated from other clusters with the same characteristics. In our stochastic model, at each step of time individuals will undergo the selective process and it will have a chance to move and reproduce – they may die from lack of food. Speciation will occur when a population remains isolated for a pre-established minimum time – this population passes to be considered new specie. A species that has no individual in the system will be considered. The carrying capacity of our system is 5000 individuals. The species will have plastic and non-plastic genotypes. The variation in phenotype of the individual will elapse of change in temperature (stimulus). Each plastic phenotype will be generated based on direct genetic expression, without any type of regulator mechanism (Via et al. 1995; Gestel e Weissing 2018) – all children inherit all the alleles from their parents, being that each one these has a chance of mutating 0.001. The selection will favor phenotypes that correspond to the environmental condition defined as ideal for this. Plastic individuals in our system will have an associated energy cost for being plastic and for producing the phenotype (DeWitt et al. 1998). A part of our chosen parameters are based on the article by Botero et al. (2014).

Besides that, we will explore the system variables to understand which parameters will affect the mechanisms of adaptation and trait divergence (Ghalambor et al. 2015), recommended by (Pfenning et al. 2010 & Bro-Jorgensen et al. 2019). We will modify: the rate of genetic mutation, the *fitness* of plastic and non-plastic traits (adaptive value), type of genetic expression (direct or probabilistic), probability of canalization and number of alternative genotypes. For each simulation with a specific combination, we will do 100 replicates. At the end of the simulations, we will count the trait evolution values, the speciation numbers and the extinction numbers. We will also verify the time necessary for the selective process has in other non-plastic phenotypes (after having acted on plastics) – this both for the case of facilitate and for difficult. We will search to understand this process temporally, as recommended by Fox et al. (2019).

*SOFTWARE*

We will use agent-based modeling (ABM) using a package called “gen3sis” in R software (R Development Core Team 2019; Hagen et al. 2021). The R software is useful for this purpose too, because, besides to being popular, it is a viable path for scientific modeling and analysis (Tippmann 2015). To communicate this model we will use the standard protocol for ABM – ODD (Overview, Design concepts, and Details) (Grimm et al. 2010).

*ANALYSIS*

We will use a linear model in R (R Development Core Team 2019) to verify if there is a relationship among plasticity and the trait evolution, speciation and extinction rates.

In this chapter, we will modify the model of chapter I to investigate the mechanisms behind how phenotypic plasticity affects adaptive evolution in different contexts.

*MODEL*

Relevant concepts for understanding this model: (a) disturbance – any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White & Pickett, 1985); (b) activational plasticity – the extent to which the phenotype of an agent varies as an immediate response to variation in external stimuli (Stamps 2016); and (c) developmental plasticity – the extent to which the current phenotype of an agent varies as a function of external experiences, stimuli or environmental conditions that occurred in the past (Stamps 2016). There will be changed from the previous model, before the beginning selective process of plastic phenotypes, the speed of climatic change (slow and fast) – a relevant disturbance to be studied today (Sih et al. 2011; Berger-Tal et al. 2016; Kelly 2019). In the model that individuals have activational plasticity, activation will occur instinctively when it appears on the ecological track. In the model with developmental plasticity, the change in the phenotype of individuals will derive from a track that will occur in their development over the generations. In the behavioral model there will be an immediate phenotypic flexibilization and in the morphological model this modification will occur over the generations. We will do 100 replicates for each parameter combination cited previously.

*ANALYSIS*

We will utilize a multifactorial ANOVA in R (R Development Core Team 2019) to know if there is a statistically significant difference among the levels of factors in trait evolution, speciation and extinction rates. The factor levels are: activational and developmental plasticity, plastic phenotype in behavior and morphology and slow and fast climate change. We will also verify if there is an interaction among these factors. We will use the Tukey test to identify where the statistically significant difference is.

**Results**

We found…

**Discussion**

As expected…

**Conclusion**

We conclude…

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**PAPER 2 (CHAPTER 2):**

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**Abstract**

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Although there are generic explanations for the understanding of how phenotypic plasticity affects adaptive evolution (facilitate or difficult), this theme remains unresolved (Kelly 2019) and it is a controversial problem (Ghalambor et al. 2015). One of the main reasons for this is the little understanding of the mechanism behind this theme and its association with current and future biodiversity patterns (Wong e Candolin 2015; Fox et al. 2019). The difficult in understanding the effect of plasticity on adaptive evolution is related to three main topics: (i) trait evolution (how it occurs, how long it lasts facilitating or making it difficult, in case of the latter, what would be the limit of hinder of plasticity for adaptation) (Wong e Candolin 2015); (ii) macroevolution (time in which it occurs and dynamic of selection of new phenotypes in case of facilitation) (Bro-Jorgensen et al. 2019; Fox et al. 2019); and (iii) the extinctions that arise during the process (Wong e Candolin 2015; Bro-Jorgensen et al. 2019; Fox et al. 2019). Studying this theme and solving problems is considered by Sih (et al. 2011) one of the great contributions that ecology and evolution can offer to the modern world, since in addition to being crucial knowledge for predicting the fate of species in the short and long term, it can help in the future to prevent and combat biodiversity loss (Ghalambor et al. 2010; Ghalambor et al. 2015; Wong e Candolin 2015; Bro-Jorgensen et al. 2019).

Due to the potential that the understanding of the theme has to increase the prediction about future environments, including those affected by human-induced rapid environmental changes (HIREC) (Bro-Jorgensen et al. 2019), it has been suggested that plasticity may affect adaptive evolution of distinct ways in different contexts (Ghalambor et al. 2015; Wong e Candolin 2015; Fox et al. 2019). Some relevant contexts are: (i) type of plasticity – activational (phenotype variation in response to present stimuli – reversible) and developmental (phenotype variation in response to past stimuli – irreversible) (Botero et al. 2014; Stamps 2016; Fox et al. 2019); (ii) behavioral (instinctive and learned) and morphological (ontogenetic) phenotype (Wong e Candolin 2015; Fox et al. 2019); and (iii) disturbance speed (Wong e Candolin 2015; Kelly 2019). It is suggested that in context of rapid climate changes there is a need for rapid adaptation of species (Fox et al. 2019; Kelly 2019). This adaptation, which by the traditional evolutionary model would not occur, due the phenotypes of individuals being plastics, may occur at a relevant time scale to the paceof the environmental changes, thus preventing the extinction of species (Fox et al. 2019; Kelly 2019).

It is expected that, in the distinct scenarios, there will be different adaptive evolution times, being important to define, what types of plasticity will facilitate (if they facilitate) the adaptation in a relevant time scale (Fox et al. 2019). It is expected that: (i) in scenarios of slow climate changes any type of plasticity will facilitate adaptation in an relevant time scale (Botero et al. 2014; Fox et al. 2019); and (ii) in scenarios of rapid climate changes the adaptive facilitation will only occur in relevant time scale in the context of activational plasticity (due to the immediate flexibility of the phenotype) (Botero et al. 2014; Fox et al. 2019).

In this paper, we have 4 chapters – 2 of theoretical modeling (chapters I and III) and 2 of empirical approaches (chapters II and IV – these will serve to confirm the predictions of the models). So, given the context established above, the goal of this project is to understand:

Chapter I – Theoretical modeling and mechanism I. Effect of phenotypic plasticity on adaptive evolution

We expect that phenotypic plasticity facilitates adaptive evolution by canalization the plastic phenotype and selecting other phenotypes.

1. Effect of phenotypic plasticity on evolution rates of the trait

* We expect that plasticity will increase evolution rates of the trait

1. Effect of phenotypic plasticity on speciation rates

* We expect that plasticity will increase the speciation rates

1. Effect of phenotypic plasticity on extinction rates

- We expect that plasticity will decrease extinction rates

Chapter II – Empirical and pattern approach I. Effect of phenotypic plasticity on adaptive evolution

We expect that the results of this chapter, obtained through empirical data, confirm the results that we found in the theoretical model elaborated in chapter I.

Chapter III – Theoretical modeling and mechanism II. Effect of phenotypic plasticity on adaptive evolution in different contexts

All contexts will facilitate adaptive evolution, however in distinct speeds.

(a, b and c) Effect of phenotypic plasticity on evolution rates in disturbance of low and fast speed.

- We expect that phenotypic plasticity will increase evolution rates of the trait, speciation rate and decrease the extinction rate independent of disturbance speed. This effect will occur more quickly in cases of activational than developmental plasticity, given that this first is a quick response and it does not depend on alternating generations – the plastic genotype will be selected, dominate the genetic pool and will be canalized faster, being useful mainly for the adaptive selection in the context of rapid disturbances as habitat loss. Genotypes that are plastic in development tend to go for the ideal phenotype (“tendentious” selection), the delay in the selective process is basically due to the fact that it occurs between generations – it will serve more for slow disturbances. The same expectation that we have for activational plasticity, we have for behavioral phenotypes – for the same reasons already mentioned, beyond of flexibility that it has in comparison with morphological phenotypes.

Chapter IV – Empirical and pattern approach II. Effect of phenotypic plasticity on adaptive evolution in different contexts

We expect that the results of this chapter, obtained through empirical data, confirm the results that we found in theoretical model elaborated in chapter III.

**Material and methods**

In this chapter, we will investigate with empirical data the effect of phenotypic plasticity in adaptive evolution, using a macroecological and macroevolutionary approach to verify patterns.

In this chapter, we will empirically investigate the effect of phenotypic plasticity on adaptive evolution in different contexts, using a macroecological approach to verify patterns. We will use the sampling information already obtained in chapter II of the work.

*SAMPLING*

We will test the predictions of the chapter 1 model using a database of developmental thermal plasticity on reptiles available in Nature 2018 (Noble et al. 2018).

We will use distinct speeds in climate change to verify effect of plasticity on adaptive evolution in different contexts.

*ANALYSIS*

The tests will be accomplished in two stages. In the first, will be tested the effect of intraspecific variation in body size on evolution through a selection of evolutionary models of continuous characters (see details in https://link.springer.com/chapter/10.1007/978-3-662-43550-2\_15) (Meara e Beaulieu 2014). To test the effect of phenotypic plasticity on speciation and extinction rates, we will use the evolutionary model BISSE (*binary-state speciation extinction model)* (Fitzjohn et al. 2009). For this, body size variation data will be classified into different plasticity levels (and absence). The result will also indicate the proper evolution rate of phenotypic plasticity.

We will use similar analysis to chapter II. However, the estimative for speciation, extinction and trait evolution rates will be done in contexts of different speeds in climatic change and in different phenotypes (behavioral and morphological). So that instead of BISSE, it will utilize the expansion MUSSE (*Multi-State Speciation Extinction Model*), which allow associating plasticity to different contexts (Fitzjohn 2012).

**Results**

We found…

**Discussion**

As expected…

**Conclusion**

We conclude…

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