Stable laws in a changing world

The explanatory structure of evolutionary theories over the centuries

Liz Pásztor
Department of Genetics, Eötvös University, Pázmány 1C, H-1117 Budapest, Hungary

Géza Meszéna
Department of Biological Physics, Eötvös University, Pázmány 1A, H-1117 Budapest, Hungary,
Institute of Evolution, Centre for Ecological Research, Konkoly-Thege Miklós út 29-33. H-1121, Budapest, Hungary

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Abstract

Successful fundamental theories are built on verifiable principles that include measurable variables. This paper shows that Darwin's inclusive theory is built on such principles and follows their rocky road into modern operational theories. Besides reproduction, variation, and heredity, Darwin's conditions of diversification also include the potential for exponential (geometric) population growth and its necessarily limited nature. The Struggle for Existence (Malthus Doctrine), the Principles of Natural Selection, Competitive Exclusion (Rule of Similar Checks), and Divergence are mere deductions from these conditions. The dynamic system theory of robust coexistence, the theory of adaptive dynamics, and the extended theory of evolution all assume Darwin's inclusive principles as essentials. Incorporating the feedbacks controlling population growth and the tradeoffs between fitness components into the core of evolutionary theory leads to the conclusion that diversification is a fundamental, inherent feature of life and provides laws that support the determination of the expected direction of evolution in any particular case.

Content

Introduction

No matter how embarrassing it is, evolutionary biologists often express deep-rooted conflicting views on fundamental issues and the dominant processes of evolution (Laland et al., 2014; Scheiner, 2010:295; Wray et al., 2014). Is diversification an essential or contingent feature of life? Does it evolve because of changing abiotic conditions? Is it a response to changing climate and geomorphology or a result of interactions between competitors, mutualists, predators and their prey, or hosts and their parasites? Does speciation mainly happen in complete geographical isolation, or does competition in large, well-connected populations drive it (Jiggins, 2006)? Is the evolution on Earth a series of contingencies, or can evolutionary biologists predict its directions (de Vladar et al., 2017)? The answers to such broad but essential questions depend on deeply-held convictions influencing a series of implicit and explicit assumptions about the fundamental mechanisms of evolution.

Given this situation, a common question is: are there immutable rules of natural processes or natural laws that can guide researchers in the ever-changing context of scientific debate? We answer this question in the affirmative, and by analyzing some of the changing features of evolutionary theory, we reveal the stability of its fundamental assumptions and inferences.

According to historians, evolutionary biology has got an important status among the exact sciences and earned a unifying role within biology due to its strong foundations in theoretical population genetics and its experimental, quantitative methods based on *genetic* theory (Smocovitis, 1992). This unifying role has only been reinforced by the rapid rise of genomics in this century, as the theory of population genetics provides the key to deciphering the genomic imprints of the evolutionary processes. However, new conceptual approaches and research lines emerged in the second part of the last century. While the interest of experimental biologists has increasingly shifted to the processes of life history evolution, species formation, and phylogenetics, in addition to the studies of genetic polymorphisms and population differentiation, theoretical evolutionary biologists began to take a more ecological approach to model evolutionary processes. The optimality and game-theoretical (ESS) models of evolutionary biology developed since the 1970s (Day, 2005) put aside the problems associated with sexual reproduction. They focused on the constraints on *trait evolution* rather than the conditions that alter allele frequencies in a sexually reproducing population (Parker and Smith, 1990). The common feature of the emerging field of Darwinian dynamics (Vincent and Brown,

2005) or adaptive dynamics (Dieckmann et al., 1996; Geritz et al., 1998) is the study of evolutionary trajectories of traits in terms of population dynamics in feedback environments. Focusing on the consequences of interactions between individuals with different alleles or belonging to different clones or species has directly embedded the evolutionary problems into community ecology. Species emerging in sympatry or parapatry must obey the rules of coexistence like limiting similarity (Meszéna et al., 2006) or exclusive resource limitation (Fretwell, 1977; Pásztor et al., 2016b:115-120). Suppose evolution occurs on the stage set up by interacting systems of populations of varieties, alleles, clones, or species (Hutchinson, 1965). In that case, feedback loops (checks on population growth in Darwin's language, population regulation in ecology, or feedback environments in the language of adaptive dynamics) should have a significant role in the play.

The difference between the genetic and ecological views of evolution is similar to the difference in Darwin's early and mature theories of the origin of species. Historians of science tend to agree (see references in Schweber, 1985) that Darwin's theory differed essentially from his earlier views when he started to compile the "*On the Origin of Species*" (*Origin* further on) in 1857. As Schweber (1985) explains, Darwin gradually changed his views on three critical points between 1846 and 1854 based on his taxonomic work on barnacles: he no longer thought that organisms "*vary exceedingly little*" (Darwin, 1909:81), he dropped the idea that the rate of evolution is determined primarily by events on the geologic or geographic time scale. He also discarded his former view that geographic isolation is necessary for divergence. In parallel to Darwin's early theory, the Modern Synthesis assumed slow evolution and explained speciation mostly in terms of geographical isolation and climatic changes. In contrast, Darwin's mature theory and the ecological theories of evolution both consider organisms in ecological interactions and trait evolution in the context of these interactions. According to these theories, geographical isolation and physical changes in the environment are important in general but not essential conditions for diversification of life.

While studying the nature of variation changed Darwin's views on the mode of evolution, he also sought a theoretical explanation. Although this critical fact is often ignored, Darwin was as much "*… a theoretical biologist in the mechanistic tradition*" (Penny, 2009) as an experimentalist and naturalist. Explanations were even more important for him than recognizing facts (Holt, 2009b). He wrote after the publication of the *Origin*: "*If you don't have a theory you might just as well count the stones on Brighton beach"* (cited in Penny, 2009). He would have felt “*awfully flat*” without a sound and general explanation of diversification based on principles. According to historians’ analyses, it was the quest for a mechanistic theory explaining the diversification of life through biotic interactions that took Darwin several years. Finally, the discovery of the “*Principle of Divergence*” (Darwin, 1872:87) made his new theory logically complete. The keystone of his theory, as Darwin called it, provided a firm solution to the problem of diversification as it is a deduction from the two pillars of his theory; the “*principle of geometrical increase”* and the “*doctrine of Malthus*” (Darwin 1872:50). Being a keystone, it also “… *distributes the weight between the core theory and the evidence for descent*” (Kohn, 2009:87). While the Modern Synthesis relied on the *Principle of Natural Selection*, it has not integrated Darwin's theory's two main *ecological* pillars and dismissed his divergence principle. As Provine (1985:826) noted, the neo-Darwinian or synthetic views “*differed substantively”* from Darwin’s views in the *Origin*.

While Darwin’s *Principle of Divergence* was rejected explicitly by Mayr (1992) and disregarded by the community of evolutionary biologists for a century (Kutschera and Niklas, 2004), it has returned from oblivion in several contexts at the turn of this century. Its empirical basis was strengthened as diversification has been observed repeatedly in several laboratory systems of microorganisms under fixed experimental conditions (Dykhuizen, 1998; Good et al., 2017; Rainey and Travisano, 1998) and is predicted to be found in many others (San Roman and Wagner, 2018). Besides historical analyses of the meaning and the role of the principle in Darwin’s theory (Kohn, 2009; Tammone, 1995), a biological monograph collected empirical evidence for competitively mediated disruptive selection and character displacement to re-evaluate the process of speciation in the light of the principle (Pfennig and Pfennig, 2012). The diversity-dependence of species formation in macroevolution was discussed as a result of interspecific competition and as a process closely related to Darwin's long-abandoned principle (Rabosky, 2013). Our ecological textbook that presents general ecology based on seven Darwinian principles also incorporated The *Principle of Divergence* in the context of niche segregation (Pásztor et al. 2016b:4, 200-3). Modeling the long-term results of frequency-dependent selection stemming from interactions between individuals has led to the discovery that evolutionary branching may not be a peculiarity but rather a typical outcome of many ecological situations (Day, 2005). This outcome is exactly what the *Principle of Divergence* and Darwin’s second theory expects.

Evolution by natural selection requires variation, heredity, and differential reproduction or survival. All of us educated in biology have learned these conditions. This paper argues that this set of conditions becomes complete only by including the necessity of population regulation (doctrine of Malthus, or the struggle for existence in Darwin’s language). An inclusive theory of evolution that explicitly acknowledges the necessity of *“the struggle for life”* contains the necessary conditions of diversification and explains a broader range of phenomena from first principles than a theory that restricts its scope to determine the conditions of natural selection. Moreover**,** we demonstrate that Darwin developed and consistently presented the principles of this theory as principles. We express and, when necessary, modify these principles in current terms of theoretical biology. We think the stability of these primary conditions (assumptions) and laws (first principles) over centuries may reflect natural laws.

In support of our proposition, we provide historical analysis and a reconstruction of the logical structure of Darwin’s mature theory in operational terms. First, we compare the logic of the core idea of the genetic approaches as presented by Lewontin (1970, 2010) and the ecological interpretations of Darwin’s theory exemplified by the summaries of Elton (1926) and (Rosenberg, 2012). Next, by revealing how Darwin made the most demanding last step of his quest for a sound theory, the paper provides evidence of his theory's often overlooked system-dynamical nature. This historical analysis based on Darwin’s texts draws on the works of Alfred Russell Wallace and several historians of science. It also goes one step further: it reveals the connections between the checks on population growth and divergence by presenting that the *Principle of Divergence* relies heavily on another principle of Darwin, which we call the *Rule of Similar Checks on Growth or simply The Rule of Similar Checks*. Based on the result of the historical analysis and the definitions of reproductive units, state variables, fitness, constraints, and tradeoffs, we formulate a basic set of conditions and laws of an observation-based, inclusive evolutionary theory that is consistent with Darwin’s mature theory and unifies the subsequent genetic and ecological approaches.

In discussing the results, we conclude that identification of the role of the interactions between individuals (feedbacks on population growth) in the logic of the evolutionary theory may provide a firm basis for further theory construction, for the evaluations of modeling results, for establishing their connections to each other and observations. If the object of study is a system of populations of interacting organisms characterized by their alleles, traits, and species (clonal) identity, the view of evolution becomes system-centric (Laland et al., 2011). The dynamics of biological systems are simultaneously regulated at several levels and timescales, from gene expression and cell growth through organismal homeostasis to population growth. Therefore, studying the evolution of organismal traits in the context of interrelated subsystems becomes a meaningful goal of inclusive evolutionary research. Brief speculation about the future perspectives of unifying and integrating biological theories closes this paper.

Evolution in genetic and ecological perspectives

Lewontin's principles

Conditions, or axioms, whatever we call them, provide the fundaments of theories built up by logical deduction and mathematical derivations from observations. The dominant scientific practices influence these "What-if" scenarios that determine how to explain evolutionary change (Gyllenberg and Metz, 2011). One way to summarize our understanding of biological evolution is to identify the conditions under which it may occur. Lewontin's principles (Table 1) are observations. They "*provide a purely mechanical basis for evolutionary change*" (Lewontin, 2010) and focus on the necessary universal conditions of the selective change of population composition from one generation to the next. This focus tightly corresponds to Sewall Wright's definition of evolution as change in allele frequencies (Wright, 1931). Endler (1986:4) expressed the relation between allele frequency change within or between generations and the three conditions of variation, inheritance, and fitness differences as a syllogism.

1. *The principle of variation*	among individuals in a population, there is variation in form, physiology, and behavior
2. *The principle of differential reproduction*	in a given environment, some forms are more likely to survive and produce more offspring than other forms
3. *The principle of heredity*	offspring resemble their parents more than they resemble unrelated individuals
4. *The principle of mutation*	new heritable variation is constantly occurring

Table 1 The four conditions of evolution by natural selection as given in Lewontin (2010). The first three conditions were introduced in Lewontin (1970).

Lewontin's principles are observation-based and metaphor-free and lack any reference to adaptation. Lewontin (2010) repeatedly argued that it is often enough to prove that a particular trait „… *confers a reproductive advantage*". One does not have to bother finding the potential causes, as countless of them exist. Evolutionary biologists should not „… *engage in idle speculation*" about adaptation as it is almost hopeless to find out what caused the advantage of one form over the other, especially in the past. Organisms construct their niches, „… *there is an infinity of ways an organism might make a living, an infinity of ways of putting together the bits and pieces of the external world*" (Lewontin, 2010). If this is true, the directions of evolution depend on chance (*contingent*), as there are many solutions for an organism to solve any problem raised by its environment (Lewontin, 1978), which, in part, they mold themselves.

Lewontin's principles do not refer to the population dynamical aspects of Darwin's theory either; evolution is abstracted away from the causes of selection, including population regulation in this formulation wittingly. As Lewontin (1970:1) wrote:

> "It is important to note a certain generality in the principles. …. No particular mechanism of inheritance is specified. …. Nor does Principle 2 specify the reason for the differential rate of contribution to future generations of the different phenotype. …. the element of competition between organisms for a resource in short supply is not integral to the argument".

In population genetic theory, the state variables are the relative frequencies of alleles whose relative dynamics are determined by the relative fitness values of genotypes (Sober, 2014:38-42, 195). Density- and frequency-dependent genotypic selection are special cases, while density-independent selection is the general "reference case" (Christiansen, 2004) within this classical framework (Mallet, 2012).

Getting rid of Darwinian metaphorical expressions such as "*natural selection*" and "*fitness,*" Lewontin also tore the last strands from Darwin's original theory. This purification, of course, does not mean that Lewontin's set of principles contradicts Darwin's theory. For example, in Scheiner's (2010:296) framework, these three conditions define a *subsidiary theory* of a more general theory of evolution.

Focusing on relative genotypic fitness and natural selection filtering intra-population variation was a non-trivial and fruitful innovation of theoretical population genetics in the early decades of the last century. However, it was not the only theoretical possibility that followed from Darwin's and Wallace's works. In the "*golden age of theoretical ecology*" (Scudo and Ziegler, 1978), Kostitzin based his models of natural selection on Lotka-Volterra's models of competition (Christiansen, 1988). Volterra and Kolmogoroff took it for granted that they studied the consequences of the struggle for existence that an article's title and some introductory sentences exemplify. Gause, who was called a member of "*the modern school of population students*" (Pearl, 1934:VI), studied the consequences of species interactions under the title "*The struggle for existence*" and referred to species and mutations alike. While Haldane based the estimation of the change in allele frequencies on selection coefficients, Gause indicated that the state variables of a Darwinian theory could be the densities of the mutants' or the species' populations:

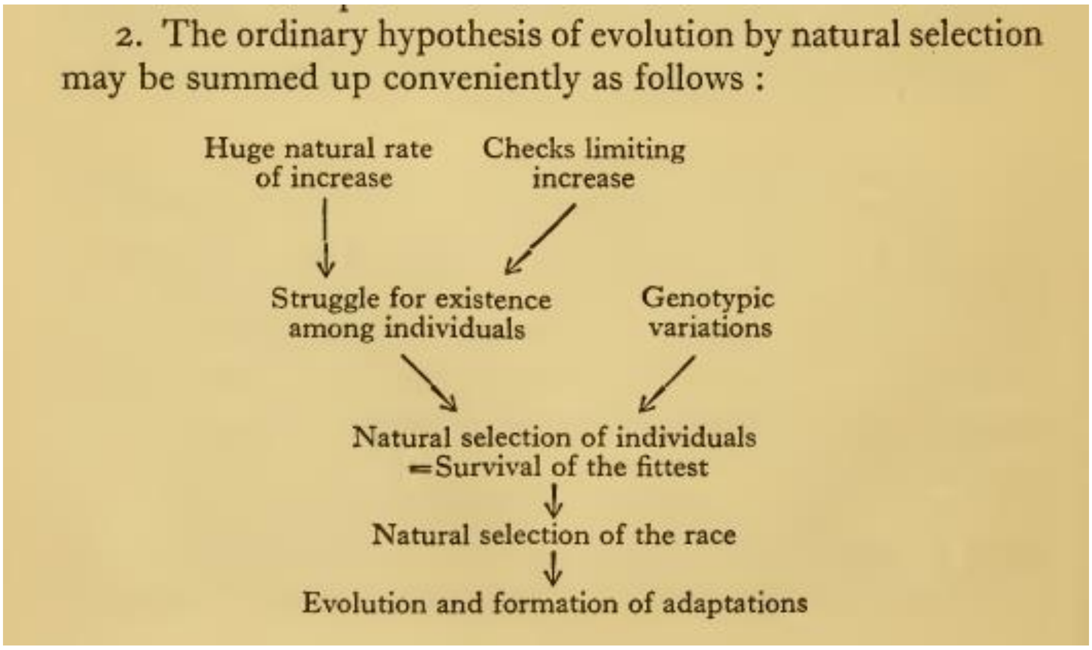
> It seems to us that there is a great future for the Volterra method here, because it enables us not to begin the theory by the coefficient of selection but to calculate theoretically the coefficient itself starting from the process of interaction between the two species or mutations. (Gause, 1934:111).

This insight of Gause and Kostitzin's works has not been integrated into the mainstream of evolutionary biology for a long while. Methods, models, and terminology of the genetic and ecological branches of population biology developed largely independently until the birth of evolutionary ecology in the sixties (Levins, 1962, 1968; MacArthur, 1961; MacArthur, 1962).

Ecological principles

After Haeckel, who defined ecology as "*the science of the struggle for existence*" (Cooper, 2003:4-6), those formulations may be safely called ecological interpretations of Darwin's theory that refer to the struggle for existence (competition). These interpretations include population dynamical concepts like the potential for exponential (huge) population growth and the *necessity* of its limitation (the necessity of population regulation). Here, we present two examples from the many to illustrate our argument. Figure 1 shows Elton's sketch of "*the ordinary hypothesis of evolution by natural selection*." Rosenberg's (2012) axiomatization presents a similar logical structure almost a hundred years later (Table 2). Although there are differences between them, both derive natural selection from competition and consider the process of natural selection as adaptation.

Besides including the population dynamic principles, the ecological approach explicitly includes species as subjects of selection in agreement with the practice in the golden age of theoretical ecology. Elton referred to both the selection of individuals and the selection of race.



2. The ordinary hypothesis of evolution by natural selection may be summed up conveniently as follows :

Huge natural rate of increase

Checks limiting increase

Struggle for existence among individuals

Genotypic variations

Natural selection of individuals =Survival of the fittest

Natural selection of the race

Evolution and formation of adaptations

Figure 1. Extract from Elton's Animal ecology (Elton, 1926:180)

Axioms	**Theorems**
A1. Reproducing populations increase exponentially.	T1. There will always be a struggle for survival and reproduction among competing populations.
A2. The capacity of any region to support any reproducing populations is finite.	
A3. There is variation in fitness of members of these populations and some of these variations are heritable.	T2. In the struggle for survival and reproduction the fittest variants will be favored and, therefore, T3. Adaptive evolution will occur.

Table 2 Alex Rosenberg's presentation of the three observations (axioms) and three conclusions (theorems) of Darwin's theory (Rosenberg, 2012:170-71)

According to Rosenberg, *"a general claim about the mechanism of evolution"* should be "*a claim about reproducing members of any line of (reproductive) descent*" (Rosenberg 2012:172). As replication copies the alleles, copies of an allele are "members of a line of reproductive descent" ("identical by descent" in population genetic terms). Conspecific individuals inherit their species identity from their parents; thus, they are members of the "species" line of reproductive descent. In the case of asexual reproduction, common descent defines the members of a clone. Accordingly, a theory should treat competition between populations of different alleles of the same gene and between populations of different species or clones alike. Hardin expressed this idea, which is missing from Lewontin's (1970) paper about the units of selection, most clearly:

> The system of discrete alleles at the same gene locus competing for existence within a single population of organisms is perfectly isomorphic with the system of different species of organisms competing for existence in the same habitat and ecological niche. (Hardin, 1960:1296).

This generality is in contrast with the narrow interpretation of Darwin's heritage that ignores the capacity for exponential growth and its limitation.

One should admit that the presented "ecological" frameworks may be annoying for anyone accepting the strict operational approach of Lewontin. As these formulations still include Darwin`s original metaphors - the struggle for existence, fitness, natural selection, and adaptation - their meanings are open to several interpretations. However, it is clear that the genetic and ecological principles have one feature in common: neither explains life's diversification without further assumptions. Why does not a single, omnipotent living being, a Darwinian demon (Law, 1979) - "the fittest one" - survive and exclude all emerging variants? The addition of the assumption of external variation in the physical environmental conditions (e.g., geomorphology, climatic conditions, chemical composition) and geographic isolation of populations are indispensable assumptions to explain the diversification of species in the context of the modern synthesis (Mayr, 1963) as well as of the ecological theories of evolution in the past century.

Darwin's explanation of diversification

Darwin's central problem

Must the conceptual core of evolutionary theory be silent about diversification –as Lewontin suggested? There is no doubt that Darwin himself wanted to explain the processes leading to the diversification of life on Earth and to work out a coherent, causal explanation derived from a set of first principles. The central question of interest for him was:

> …how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? (Darwin, 1859:61; 1872:48).

Darwin’s question goes beyond the more straightforward problem of adaptation to specific environmental conditions in isolation. Darwin wanted to understand the divergence of forms in the context of their relations.

Darwin`s *“Big Species Book*”, prepared from September 1854 to June 1858, reflects the major changes in his thinking about the causes of diversification (Kohn, 2009). He switched to the view that biotic interactions drive evolution and direct effects of the physical environment play a secondary role only (Darwin, 1975:271-2). He also argued that the “manufacturing of species” occurred in large populations of vast open areas rather than on small islands (Darwin 1975:262). Competition for food or space and against natural enemies instead of climate determine the geographic distribution of species (Kohn, 2009; Reznick and Ricklefs, 2009). Finally, he explained that selection prefers those forms which either occupy empty places in the “economy (polity) of Nature” or perform better than the predecessors that occupied the place (Pearce, 2010). By the publication of the *Origin,* ceaseless selection and diversification in response to changes in species abundance had become a *logical necessity* for Darwin. The explanation relied on four principles and a corollary: the *Principle of Natural Selection* (Darwin, 1872:49), the *Principle of Divergence* (*ibid*:87*)*, the *Principle of the Division of Labour* (*ibid*:74), and the *Rule of Similar Checks* (*ibid*: 58-9) with the corollary about the evolution of characters (*ibid*:60).

The importance of the *Principle of Divergence* in Darwin’s theory cannot be overemphasized. It made the explanation of diversification logically complete. According to Tammone:

> Darwin regarded the principle of divergence, along with the concept of natural selection, as the "keystone" of his work. Without a keystone, of course, an arch collapses. Without an understanding of the principle of divergence, so, necessarily, does our understanding of the Origin of Species. I think the meaning of this important principle deserves our careful reconsideration. (Tammone, 1995:131)

However, reconsidering is not an easy task as formulating the principle is metaphoric and relies on a complex argument. Biologists usually focus on its ecological aspects, while historians include its relations to the concepts of progress (Ghiselin, 1999), the tree of life (Kohn, 2009; Tammone, 1995), the economy of nature, and the division of labour (Pearce, 2010). Here we reconstruct the conceptual framework (sensu Scheiner, 2010:293) of Darwin’s theory based on the close analysis of his texts and former works of historians.

We should be aware of some difficulties when reconsidering Darwin's core theory. As he was both a uniformitarian and a gradualist (Hallam, 1983), his general statements and explanations often implicitly cover several processes on several timescales. His final wording of the *Principle of Natural Selection* in the 6th edition shows this clearly:

> Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow from the struggle for life. Owing to this struggle, variations, however slight, and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals, and will generally be inherited by the offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, …. (Darwin 1872:48-49).

The events of an individual's life history, the change in population composition from one generation to the next, and the outcome of these processes after many generations define three different timescales, all covered by this passage. Examples supporting the general argument usually help identify the timeframe in question. With this in mind, we can reveal the explanatory core of Darwin's theory of diversification.

The Rule of Similar Checks

Biologists' standard interpretation of the *Principle of Divergence* emphasizes that divergence requires a difference in "*ecological requirements*" as it lessens the strength of competition. Ernst Mayr, who was the harshest critic of Darwin's species concept (Mallet, 2008), summarized the meaning of the *Principle of Divergence* accordingly:

> The basic point of the principle of divergence is simplicity itself: the more the co-inhabitants of an area differ from each other in their ecological requirements, the less they will compete with each other; therefore, natural selection will tend to favor any variation toward greater divergence. The reason for the principle's importance to Darwin is that it seemed to shed some light on the greatest of his puzzles-the nature and origin of variation and of speciation. (Mayr, 1992:344).

The more elaborate and favorable discussion of Reznick and Ricklefs (2009) has the same interpretation almost two decades later:

> Darwin’s principle of divergence derives from what he thought to be one of the most potent components of the struggle for existence. He argued that the strongest interactions would be among individuals within a population or among closely related populations or species, because these organisms have the most similar requirements. Darwin’s principle of divergence predicts that the individuals, populations or species most likely to succeed in the struggle are those that differ most from their close relatives in the way they achieve their needs for survival and reproduction. (Reznick and Ricklefs, 2009:838).

Already Gause explained Darwin’s idea similarly:

> … the intensity of competition is determined not by the systematic likeness, but by the similarity of the demands of the competitors upon the environment. (Gause, 1934:19).

Thus, the consensus assumes that Darwin’s simple idea was that the strength of competition increases with the similarity of requirements.

Darwin qualified his thesis as a “*general rule*” (Darwin 1975:201). Wallace, having repeated Darwin’s argument, called it a principle:

> As an effect of this principle, we seldom find closely allied species of animals or plants living together, …” (Wallace, 1889:34-5).

This rule is central to Darwin’s argument as it logically links his two fundamental principles of natural selection and divergence. Therefore, it is essential to understand what makes two varieties or species similar in Darwin’s argument. His texts show that he had a clear understanding of the kind of similarity he referred to. His concept differed in a subtle but essential way from the broad “species are similar if they have similar ecological requirements” interpretations. Several of his texts support the understanding that he considered two varieties similar if their populations are checked similarly, as we show step by step in the following paragraphs.

In the last part of the third chapter introducing the struggle concept in the *Origin*, Darwin`s argument starts with a description of interactions between individuals, which defines the shortest time scale and continues with the population-level consequences on a longer one:

> … the struggle almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers. In the case of varieties of the same species, the struggle will generally be almost equally severe, and we sometimes see the contest soon decided.” (Darwin 1872:58-59).

In the first part of the argument, Darwin enlists two broad classes of environmental factors that may regulate a population’s growth by feedback loops: resources (*district*, *food*) and natural enemies (*dangers*). “Dangers” means natural enemies here, as Darwin explained and illustrated by examples that interactions check population growth, not the weather conditions apart from extremely harsh habitats (in sink populations) (*ibid*:53-8). He related the strength of competition to the regulating factors (agents: predators, prey species, pollinators, parasites) shared by them - expressing his ideas in actual ecological terms (Krebs, 2001; Pásztor et al., 2016b). Members of the same species living in the same place share all the regulating agents; therefore, the contest is strongest among conspecifics. Varieties may also share many checks on population growth; consequently, they also compete vigorously. The population-dynamic consequence of the similarity of population regulation is “extermination” or “extinction” of the weaker variety or species.

> To keep up a mixed stock of even such extremely close varieties as the variously coloured sweet-peas, they must be each year harvested separately, and the seed then mixed in due proportion, otherwise the weaker kinds will steadily decrease in numbers and disappear. (*ibid*:59).

Thus, this rule qualifies the *Principle of Natural Selection* as it identifies the condition when the “*preservation of favourable individual differences and variations, and the destruction of those which are injurious*” Darwin (1872:63) means the survival of a single variant. In other words, it adds a condition for the outcome of the “struggle for existence” over several generations. A single variant will exclude all the others if the competitors are similar in frequenting the same districts, requiring the same food, and being exposed to the same dangers. Only a single variant remains if the varieties or species have the same checks on the growth of their populations. As far as species are concerned, this process is called competitive exclusion in ecology (Hardin, 1960), and we call it the “*Rule of Similar Checks*” in this paper. The term “ecological requirement” does not differentiate between regulating and non-regulating environmental conditions, while the conditions listed by Darwin are all considered as ones that may control population growth.

Divergence of characters and the corollary to the Rule of Similar Checks

Darwin designed the divergence principle to explain diversification in the “structure, constitution and habit,” i.e., characters (traits) of the organisms; thus, competition for food in the face of “dangers” had to be related to the *divergence of character*. Therefore, having introduced and discussed the similarity rule, Darwin continued the argument with a corollary:

> A corollary of the highest importance may be deduced from the foregoing remarks, namely, that the structure of every organic being is related, in the most essential yet often hidden manner, to that of all other organic beings, with which it comes into competition for food or residence, or from which it has to escape, or on which it preys. (Darwin 1872:60).

The factors inducing competition listed in this claim, i.e., food, residence, predators, and prey, are the same as those listed in the *Rule of Similar Checks*; district, food, and dangers. In its more detailed explanation, the "*Big Species Book*" relates structure, habits, and constitution one by one to the interactions between species and climate.

> It follows almost necessarily from what we have seen of the struggle for existence, dependent on the habits of animals & plants, that the structure of each organic being stands in most intimate relation to that of other organisms. For habit generally goes with structure, not withstanding that in most great families, a few species having the same general structure can be picked out with habits in some degree aberrant. …..Obviously every living being has its constitution adapted to the climate of its home; but this seems to produce scarcely any visible difference in structure: thus in every kingdom we have a few species keeping identically the same structure under the most opposite climates—…. if we run over in our mind the various structures of the commoner animals, we shall see that the manner of obtaining their prey or food & of escaping danger from other living beings is almost equally influential on their structure (Darwin, 1975:208-9).

Thus, those factors or agents determine the structural traits and habits of the organisms they may compete for or against, i.e., food and enemies when they live in the same place.

Darwin also linked the *Rule of Similar Checks* and the *Principle of Divergence* explicitly in the fourth chapter of the *Origin* by repeating the very same expression introduced in the corollary:

> The forms which stand in closest competition with those undergoing modification and improvement, will naturally suffer most. And we have seen in the chapter on the Struggle for Existence that it is the most closely-allied forms, —varieties of the same species, and species of the same genus or of related genera, —which, from having the same structure, constitution, and habits, generally come into the severest competition with each other; consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them." (Darwin 1872:86).

However, competitive exclusion in itself does not explain diversity.

> How, then, does the lesser difference between varieties become augmented into the greater difference between species? - asks Darwin (*ibid*:86).

His answer is that divergence of character and extinction of the intermediate forms originate

> from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize

> on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers. (*ibid*:87).

The critical point here is that those varieties are "*enabled to increase in numbers*" in the presence of each other, which have different "*structure, constitution, and habits"* that is, which do not *"require the same food"* and which are not *"exposed to the same dangers".* This population dynamical approach, indicated by the "increase in numbers" phrase, and a complete population-dynamical argument appeared first in the second edition of *The Voyage of the Beagle* (Darwin, 1845:175), and the term became a frequent expression in the Origin.

Building a close link between the divergence principle and the similarity rule was the final step of a long process of theory construction. The first sketch of this new theory was outlined in a letter to Asha Gray from September 1857 (Darwin, 1857). However, it did not contain either the similarity rule or its corollary. Robert C. Stauffer, who transcribed and edited Darwin's hardly readable folios written between 1856 and 1858, could date some of them due to a change in the paper used. According to him, Darwin added forty extra folios to the original two on extinction and divergence between April 18 and June 12 of 1858, i.e., after a year of completing the chapter on natural selection and just before receiving Wallace's letter (Darwin, 1975:213). In this addendum, he integrated various modules of his theory for the first time (Browne, 1980).

As Browne (1980) and Costa (2017) documented, this theory construction was intertwined with intensive and persevering empirical work: calculations of botanical arithmetic to show whether larger genera contain a higher number of varieties (Ariew, 2022); observing seedlings' survival in a palm-sized bare plot to document the struggle between species; flowering plant survey to estimate species diversity in a uniform field; the Lawn Plot Experiment where succession was followed in a small fenced, unmown plot of lawn in Darwin's garden (Costa, 2017). These studies confirmed Darwin's conclusion that diversity of structure means more life (Kohn, 2009) and supported the final formulation of the *Principle of Divergence* (Browne, 1980).

Evolutionary tree, place in the economy of nature, and division of labour

The *Rule of Similar Checks* and the *Principle of Divergence* should provide a basis for the causal explanation for why species "*form distinct genera and other higher groupings*". However, not only divergence but gaps between species and genera and a permanently growing and branching tree of life also had to follow from the struggle for existence. (Tammone, 1995:122). The ecological and taxonomical visions have to be united:

> The principle of divergence united this ecological vision with Darwin's complementary view that evolutionary history can be read in the irregular branching of the taxonomic tree of life (Kohn, 2009:87).

Darwin introduced the *Principle of Divergence* through examples and a general argument. His central example of diverging slim or robust wolves hunting deer versus sheep in the Catskill mountains first appeared in his notes only in the *Big Species Book* (Darwin, 1975:220-1). It arches over several time scales. It equally describes the variation of wolf types, episodes of their life, and the potential long-term consequence of selection: the evolution of two diverged forms differing in structure, habit, and characteristic prey. As a general explanation of the principle, he supplemented this example with an analogous, hypothetical one in the *Origin*. The generalization also includes references to processes on several time scales:

> Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural power of increase be allowed to act, it can succeed in increasing (the country not undergoing any change in conditions) only by its varying descendants seizing on places at present occupied by other animals; some of them, for instance, being enabled to feed on new kinds of prey, either dead or alive; some inhabiting new stations, climbing trees, frequenting water, and some perhaps becoming less carnivorous. The more diversified in habits and structure the descendants of our carnivorous animals become, the more places they will be enabled to occupy. What applies to one animal will apply throughout all time to all animals—that is, if they vary—for otherwise natural selection can effect nothing (Darwin, 1872:87-8).

Darwin developed his explanation by linking the familiar concepts of the economy or polity of nature and the *Principle of Division of Labour* with the new *Rule of Similar Checks*. The idea that each species occupies a particular place in the economy of nature was a common metaphor applied widely by Darwin's contemporaries. As Pearce (2010) documented, it appeared in Darwin's notes even before the concept of natural selection, unlike the *Rule of Similar Checks*, which was a late achievement. Pearce (2010:518) showed that the meaning of the metaphor changed over history from "*Linnaeus' theologically planned economy*" to Lyell and Darwin, for whom *„the economy of nature is dynamic and subject to infinitely complex interactions"*. Darwin's examples and repeated explanations indicate that, in his final view, the potential checks of a population's growth determine a place in the economy of nature in an area: the potential microhabitats, resources, and natural enemies. Wallace interpreted Darwin's ideas in the same vein by connecting the "place" metaphor with the three types of checks on population growth directly:

> The reason why this kind of struggle goes on is apparent if we consider that the allied species fill nearly the same place in the economy of nature. They require nearly the same kind of food, are exposed to the same enemies and the same dangers. Hence, if one has ever so slight an advantage over the other in procuring food or in avoiding danger, in its rapidity of multiplication or its tenacity of life, it will increase more rapidly, and by that very fact will cause the other to decrease and often become altogether extinct (Wallace, 1889:34).

When nature provides "offices to fill up" or "places to seize," which form is the best for the task? The solution was in the spirit of the age (Ghiselin, 1999; Pearce, 2010; Tammone, 1995). Darwin presented it by applying Milne-Edwards' principle of the division of physiological labour to the interactions of species in nature. Milne-Edwards principle brought an analogy between the organs in a body and human workers in a factory, while Darwin applied the analogy to species (Pearce, 2010):

> The advantage of diversification of structure in the inhabitants of the same region is, in fact, the same as that of the physiological division of labor in the organs of the same individual body—a subject so well elucidated by Milne Edwards. No physiologist doubts that a stomach by being adapted to digest vegetable matter alone, or flesh alone, draws most nutriment from these substances. So in the general economy of any land, the more widely and perfectly the animals and plants are diversified for different habits of life, so will a greater number of individuals be capable of supporting themselves (Darwin 1872:89-90).

Thus, specialization means greater efficiency, making it possible "to increase in numbers" and seize a place in the economy of nature, to the detriment of less specialized varieties. A higher degree of species specialization entails greater perfection by analogy with workers or organs (Tammone, 1995). A more specialized species excludes the less specialized, worse ones. As the complex interactions between species offer and evolution create distinct ways of making a living (places to occupy), selection leads to higher biomass and increased differences between the existing species by favouring the extreme, more specialized varieties and eliminating the intermediate ones.

Having considered all these arguments, Darwin was rightly pleased with this solution as he could derive the necessity of diversification and branching from a handful of principles.

The reconstructed logic of Darwin's core theory

Darwin was a great theorist who strove for a logically consistent and complete explanation for the diversification of life. The mosaics of his theory tightly fit together and depict a picture that differs significantly from the mainstream theories of evolutionary biology or ecology of the twentieth century. **Figure 2** shows the logical structure of Darwin's core theory: reproduction entails the capacity for geometric population growth, checked by resources (appropriate stations or food, prey) or enemies (dangers). The logical consequence of this generalization of *Malthus' principle* is that many individuals must die in each generation without producing any offspring. Experience shows hereditary differences between individuals of the same species, among which those can survive and produce offspring that have favourable characters (*Principle of Natural Selection*). This process replaces the original variants when the individuals have similar structures and habits as they compete for the same resources and share their enemies (*Rule of Similar Checks*). Otherwise, the struggle for existence produces divergence (*Principle of Divergence*). There are many new ways of making a living in the polity of nature; there are many changing places in the economy of nature produced by *the "infinitely complex relations"* between organic beings and their "*physical conditions of life"*. Those varieties and species will win in the battle for these positions or places that are most specialized in the requirement of a given job or place (*Principle of Division of Labour*).

This explanation is logically coherent and perfectly embedded in contemporary science, as revealed by a series of works by historians of science. The new features of the present reconstruction of Darwin's core theory compared to the historians' interpretations emphasizes its population dynamical aspects and clarify the logical relation between the *Principle of Natural Selection*, the *Rule of Similar Checks*, and the *Principle of Competitive Exclusion.* Darwin's examples and explanations clearly show that he considered the interaction between populations as checks on population growth, which regularly leads to selection driven by competition and extinction when individuals compete against the same limits.

The differences between Darwin's framework, Lewontin's (**Table 1**), and Elton's (**Figure 1**) are striking. **Figure 2** indicates which elements became parts of the genetic or ecological interpretations of the theory of natural selection. Lewontin's conceptualization covers just a single generation, while the ecological versions cover at least two timescales: one determined by interactions between individuals and another which belongs to the interactions between populations of "races" or "variants". However, none is stretching out for the complete branching tree of life as Darwin's theory. The explanation of inherent diversification was lost in the twentieth century.

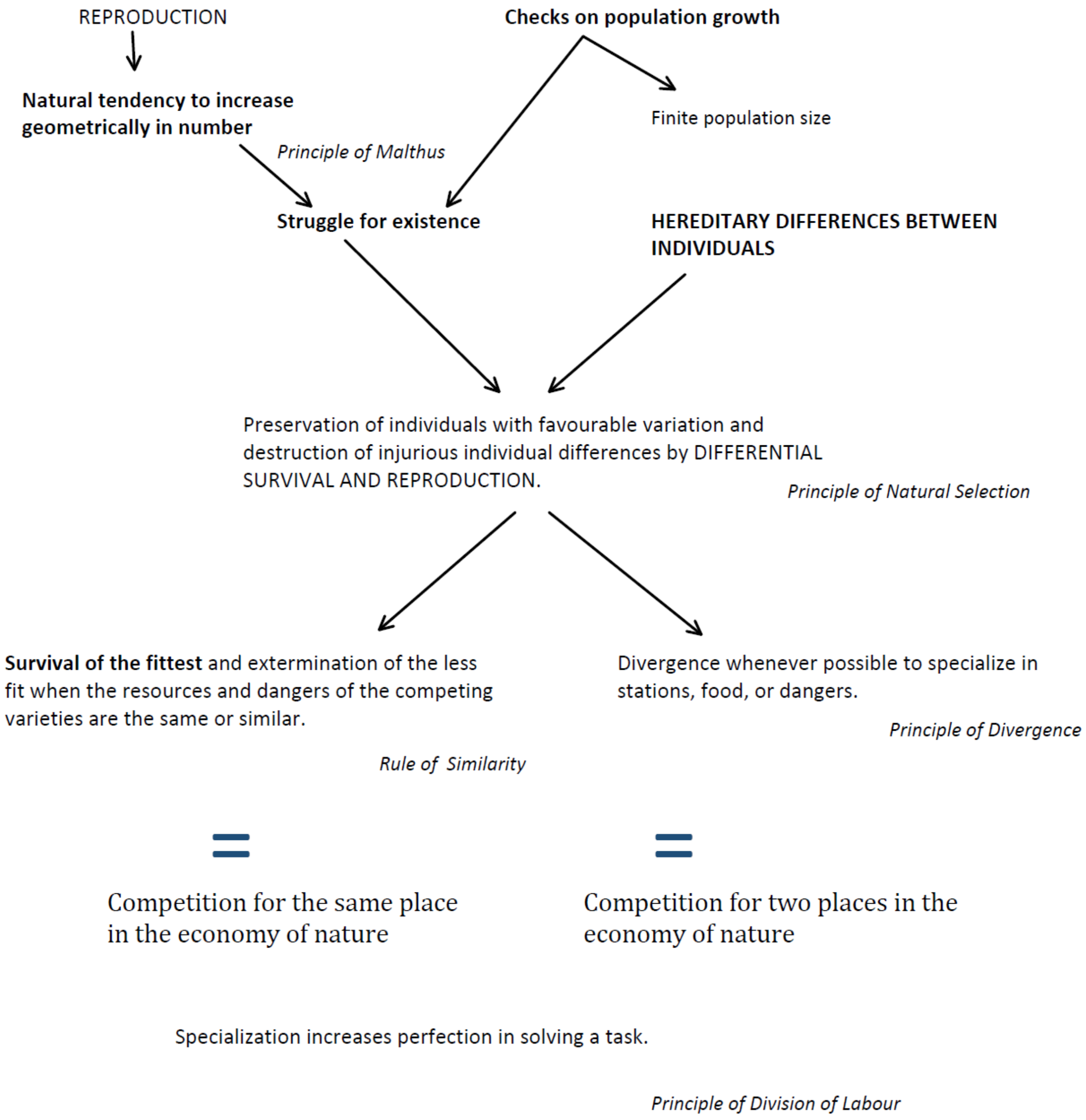


Figure 2 Framework of Darwin's core theory using his expressions. The names of the principles are in italics. Elements in agreement with Lewontin's framework are in capital letters; those that coincide with Elton's scheme are bold. Arrows denote inferences. (e.g., Because of reproduction, there is a natural tendency to increase geometrically in number, …) = signs represent metaphors corresponding to the *Rule of Similar Checks* and the *Principle of Divergence*.

An inclusive set of evolutionary principles in up-to-date form

Diversification stemming from limited population growth and interactions between organisms is an essential element of Darwin’s theory, logically derived from observations and principles. Developments in theoretical evolutionary biology and the theory of coexistence allow us to free Darwin's principles from metaphors and back them up with models and mathematical theory. In order to establish the common principles of the ecological and genetic theories of evolution, it is necessary to define their common subjects and state variables and to discuss contemporary notions of reproductive units, population-dynamic fitness, feedback, frequency dependence, and tradeoffs.

Reproductive units

Reproduction is an essential feature of life. A fundamental question about reproduction is what exactly bacteria, cells, and organisms replicate, as natural selection leads to evolutionary changes when it works on inherited variation. The attributes inherited in the offspring by division, clonal or sexual reproduction are called *units of replication* (Sober, 1984:249-55) or *reproductive units* (Pásztor et al., 2016b:16-7). Nearly faithful clonal and sexual reproduction (Metz et al., 1995) produce different reproductive units. Clonally reproducing organisms replicate their whole genome, thus their clonal-type or clonal-kind. Consequently, a clonal kind is a reproductive unit. Sexually reproducing individuals do not replicate their entire genome. Genotypes of diploid individuals are temporary allele combinations not inherited in sexually reproducing populations; thus, genotypes are not reproductive units in this case. However, sexually reproducing organisms replicate their non-recombined DNA segments and their gene-type (alleles) and also inherit their species-type (species-identity) when their offspring still belong to the same species (breeding community). As Vellend (2010:188) explained in his conceptual synthesis of community ecology

> The species identity is a categorical phenotype, assumed to have perfect heritability, except when speciation occurs, after which new species identities are assigned (just as mutation changes the identity of an allele).

Thus, the reproductive units produced by sexual reproduction are gene-types and species-kind.

Although all these attributes are inherited, i.e., they are reproductive units, the dynamics of their populations are determined by different processes on different time scales. Epistatic interactions, clonal interference, and individual-level interactions shape their dynamics in various ways. While mutations may change the identity of a reproductive unit in a single step, speciation in a sexually reproducing population is a multi-step process shaped by several interactions at various levels of the organization.

In the genomic era, haplotypes, i.e., the set of alleles located closely on a single chromosome and tend to be passed to the offspring together, are also investigated as reproductive units. The *carbonaria* haplotype of *Biston betularia* in Britain (Grant, 2012) and the lactase persistence haplotypes in several human populations (Tishkoff et al., 2007) are well-known examples.

The state variables and their dynamics

A unified theory based on common principles uses the number of individuals (population densities) as state descriptors. Reproductive units with higher population growth rates increase in numbers relative to the variants with lower ones. Therefore, the long-term per capita population growth rates, *pgr*s, (Pásztor et al., 2016b:42-3; Sibly et al., 2002) can be used in place of fitness, defined in each case under the relevant environmental conditions and time scale. The reproductive unit with higher *pgr* excludes the ones with lower *pgr*s. This population dynamical fitness measure is a widely applied one among clonally reproducing individuals, alleles, and species characterized by certain traits and ecological conditions (Brown, 2016; Charlesworth, 1994; Lande, 1982; Lande et al., 2009; McPeek, 2019; Metz et al., 2008; Pásztor et al., 2016b). Definition of fitness as the population growth rate is just a generalization of any definition based on survival and reproduction, as the asymptotic population growth rate is determined by and can be calculated from birth and death rates in any stage-structured population, at least in principle (Caswell, 2001; Metz et al., 1992).

As Sober (2014) discussed from several standpoints, fitness is *not* an individual trait that *leads to* particular survival and reproductive success but a consequence of the interaction between the individual organisms having certain traits and their environments. Consequently, the fitness of a reproductive unit characterized by a particular trait describes its fate (increase, decrease, or maintenance) always in the context of the environment of its population, i.e., generically, the *pgr* of reproductive units is a function of the environmental conditions that modify or regulate their growth.

Reproductive units are considered *equivalent* if they have *exactly* the same fitness function. Thus, any difference in their associated traits must be neutral, i.e., lacking any different effects on their *pgr*. Apart from recurrent mutations, the only stochastic processes determining the relative dynamics of equivalent reproductive units are called genetic drift for alleles and demographic stochasticity for populations of conspecifics.

In population genetics models, the state variables are the relative frequencies of alleles that can always be calculated from the absolute frequencies. Fitness is usually defined for genotypes as reproductive success (Maynard Smith, 1998:38) in the context of specific models (see Orr, 2009 for a summary). However, as genotypes are not reproductive units, one cannot expect, e.g., that a heterozygote with the highest genotypic fitness excludes the homozygotes in the long run. In correspondence, a general theory of multilocus evolution can be built only at the genic level (Kirkpatrick et al., 2002).

It depends on the actual situation and the problem to be solved, which type of reproductive unit should be chosen to study community dynamics and evolution within it (Meyer et al., 2006; Yoshida et al., 2007). Reproductive isolation of sexually reproducing populations produces isolated gene pools whose dynamics have often been determined separately from their genetic composition, like competitive experiments between species exemplify (Pásztor et. al. 2016:121-31). On the other hand, revealing genomic patterns makes it also possible to estimate selection intensity on haplotypes directly without estimating phenotypic and genotypic fitness (Chen and Slatkin, 2013).

Interactions, feedback loops, and frequency-dependence

As often emphasized in evolutionary biology and ecology, organisms require phenotype- or species-specific external conditions for survival and reproduction, which influence the dynamics and distribution of their populations (ecological tolerance (Andrewartha and Birch, 1954; Mueller-Dombois and Ellenberg, 2003) or requirement (sensitivity) niche (Chase and Leibold, 2003; Holt, 2009a; Meszéna et al., 2006). It is also a basic observation and is considered a first principle of biochemistry that living organisms are open systems (Nelson and Cox, 2017). They constantly influence their environments through metabolic activity and affect their resources and enemies through their changing behavior and physiological responses (impact niche; Leibold, 1995; Meszéna et al., 2006). Besides consumptive negative or positive interactions, organisms can deteriorate or facilitate each other's existence. For example, when they affect their surroundings, that decreases or increases the chances of other organisms' survival or reproduction.

Some of these interactions create feedback loops, including the populations' *pgrs* and densities. Any environmental variable which is an element of such a feedback loop is called regulating variable to tell it apart from the ones which are not. After decades of debate (Cooper, 2003), the issue of population regulation was settled in the first decade of this century (Sibly et al., 2002; Turchin, 2003). Mathematical theory and estimation of the long-term population growth rates from almost two thousand abundance time series demonstrate that long-term persistence means *exactly* zero expected growth rates (Brook and Bradshaw, 2006). As the probability that a continuous random variable takes a specific value by chance is zero, negative feedbacks must dominate in communities of coexisting reproductive units. The organisms' impacts on and sensitivity to the regulating variables of their populations realize the control of population growth (Figure 3).

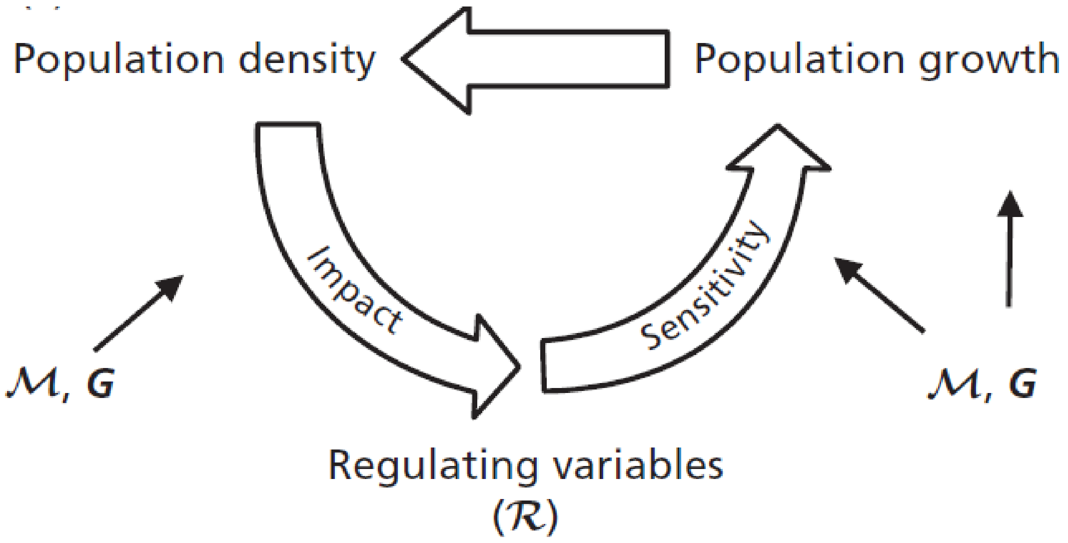


Figure 3 Living organisms depend on and affect their environment. Negative feedback through the changing quantities of external regulating variables (R) regulates their populations. The quality of environmental conditions (M, modifying variables) and genetic effects (G) modify this feedback loop (Meszéna et al., 2006; Pásztor et al., 2016b:14-6).

While the interactions between the organisms may create complex population dynamics (Abrams and Shen, 1989), a consequence of the necessity of population regulation is that the existing reproductive units have zero population growth rate in the long run, while the excluded ones have negative *pgr*s.

The *Principle of Competitive Exclusion* that closely follows from the limited nature of any population growth seems trivial for many, as Hardin (1960) discussed so convincingly. Still, it was debated heavily over decades (den Boer 1986), then disappeared from the cornerstones of ecology for a while (Levin et al., 2009) to reclaim its central place in theoretical ecology slowly (Barabás et al., 2018; Chesson, 1991; Chesson and Huntly, 1997; Fox, 2013; Meszéna et al., 2006). Many models demonstrate the principle's validity when competing units share a common regulating factor. Three principles directly follow from the competitive exclusion principle: the K-maximization (Charlesworth, 1971; Roughgarden, 1971), the R*-rule (Tilman, 1981), the P*-maximization principle (Holt and Lawton, 1994) in the case of implicit modeling of population regulation, and explicit modeling of resource competition and apparent competition, respectively. Metz et al. (2008) formulated these principles as a single pessimum one. That reproductive unit will win the competition which tolerates the worst conditions: the highest population density, the lowest resource level in case of resource competition, or the highest density of the natural enemy in case of competition mediated by it. Environmental variability and spatial heterogeneity provide opportunities for coexistence but do not invalidate the principle (Chesson, 2000; Chesson and Huntly, 1997). In Chapter 7 of our textbook, Pásztor et al. (2016b), we thoroughly discuss the objections previously raised against the principle.

The quantities/densities of the regulating variables depend not only on the quantity but also on the quality of those organisms which affect them (see e.g. the R*-rule in Tilman, 1982). As survival and reproduction are sensitive to the level of these regulatory factors, the *pgr* of a reproductive unit within a community depends on the composition of the community, thus on its relative frequency when the regulating factors are changed differently by different reproductive units. Consequently, besides the unavoidability of population regulation, frequency-dependent population growth is also a generic consequence of the interactions between living organisms with different traits, affecting each other’s living conditions differently. Frequency-dependent *pgr* of reproductive units means frequency (abundance)-dependent fitness and selection also among species within a community (Pásztor et al., 2016b:170-8; Vellend, 2010).

In the face of the threat of competitive exclusion, frequency-dependent fitness functions open up the opportunity for stable coexistence of non-equivalent reproductive units. The conditions of coexistence of reproductive units can be given in terms of negative frequency-dependence and the invasion criterion (Grainger et al., 2019), as well as in terms of the regulating factors or agents and the characteristics of the controlling feedback loops in equilibrium (Barabás, 2017; Leibold, 1995; Meszéna et al., 2006; Tilman, 1982). While the analysis of feedback loops refers to small perturbations of the densities, the invasion analysis assumes large ones: pushing down some of the densities to zero. These methods lead to the same results when the dependence of the *pgr*s on the densities is monotonous. However, in the presence of, e.g., an Allee effect, coexistence is possible by negative frequency dependence around the stable equilibrium state, but it is unreachable by invasion from low densities. The analysis of feedback loops quantifies "*ecological similarity*" in terms of the similarity of the impacts on and sensitivities to the changes in the amount (density) of the regulating factors and their dependence on the modifying environmental or genetic effects (Barabás et al., 2014; Meszéna et al., 2006).

Besides the stability of the coexistence of reproductive units, the study of its robustness (structural stability) informs about the expected changes in community composition or long-term evolution. Ecologically similar non-equivalent reproductive units may stably coexist if their fitness decreases with their frequency. However, their coexistence will be sensitive to changes in the circumstances influencing their fitness functions (Barabás et al., 2014). For linear and non-linear feedbacks analytically in a model-independent way, it was shown that negative frequency-dependence may result in robust enough coexistence of reproductive units if the impacts and sensitivities of the coexisting populations, i.e., their regulating feedback loops are sufficiently different (Meszéna et al., 2006). As a consequence of this *Principle of Robust Coexistence*, even if two similar species may converge while competing for common resources (Germain et al., 2018; McPeek, 2019), the coexistence of these species will be less and less robust, and one of them is expected to exclude the other in the long run (Pásztor et al., 2020). Darwin relied on the "place in the economy of nature" metaphor when he described the situation in which he expected the divergence of characters. A mathematical theory that provides the general conditions of robust coexistence can replace the "place in the economy of nature" metaphor with quantitative concepts.

There have been many population geneticists and ecologists who emphasized early on that the dominant form of natural selection must be frequency-dependent because of interactions among individuals: predators often prefer common prey species, parasites are adapted to common forms of hosts, and species sharing resources affect each other via their trait-dependent resource utilization functions (Antonovics and Kareiva, 1988; Christiansen, 1988; Clarke, 1979; Mallet, 2012; Rosenzweig, 1978). However, many models of frequency-dependent selection, even those that investigated the consequences of regulated population growth (e.g., Anderson, 1971; Smouse, 1976) following MacArthur (1962), were developed without taking into account the ecological drivers of selection explicitly (Mallet, 2012).

In contrast, frequency dependence is an essential, inseparable property of the theory of adaptive dynamics as it studies the initial increase of a mutant, i.e., its *invasive fitness* as a function of the feedback environment (Brown, 2016; Metz, 2012). The form of the fitness function is the consequence of the applied ecological model. The selection might be independent of the relative frequency of the competing non-equivalent reproductive units only when a single, common regulating variable controls their population growth (Heino et al., 1998; Pásztor et al., 2016b:123).

The coexistence of species and clones is often made possible by spatially heterogenous or temporary changing environments providing opportunities for different ways for population regulations, i.e., for negative frequency-dependent *pgrs* (Chesson, 2000). Such mechanisms can also maintain genetic polymorphisms within species (Fitzpatrick et al., 2007). However, frequency-dependent *pgr*-s of alleles are often induced not by external conditions but by interactions between allelic effects, e.g., on such organismal traits as resistance to a parasite (Ferreira et al., 2011). Any part of an organism's genome can influence the population dynamics of an allele through dominance interactions between homologous alleles and epistatic interactions between alleles at different loci. Quantitative genetics considers all the effects of changing assortments, „pairing and separation" of genes on fitness as effects of the within-individual environment decomposed into additive and non-heritable dominance and epistatic interactions between alleles of various genes (Barton et al., 2007:387-92).

Integrating the coexistence problem into evolutionary ecology and the increasing importance of ecologically induced frequency-dependence in evolutionary genetics have brought significant changes toward integrating formerly separate fields and thinking. Creating and modeling multiplayer systems with overlapping ecological and evolutionary time scales (Ellner, 2013) and the integration of ecologically induced frequency-dependent selection into the presentation of the standard theory of evolution (Barton et al., 2007) are just two representative examples of these processes.

Constraints and tradeoffs

What are the rules that govern the nature of variation? According to the "division of labor" metaphor, organisms must play their role in the economy of nature more and more perfectly due to the struggle for existence. Evolutionary ecologists and developmental biologists developed some operational concepts in place of this metaphor. Robert MacArthur (1961) replaced it with the “jack-of-all-trade is a master of none” simile, and Richard Levins (1962) worked out the concept of fitness sets and the *Principle of Allocation* (Levins, 1968:15). It expresses the notion that adaptation has its limitations by stating that the fitness set of a species is constrained in any spatially or temporarily changing environment. The niche theory of Chase and Leibold (2003) also relies on this assumption.

Another research line within evolutionary ecology related to observations on geographic variations of clutch size of bird species (Moreau, 1944) and its explanation (Lack, 1965) is focused on functional constraints on life-history evolution. Optimal life-history theory systematically analyzed the potential consequences of tradeoffs among such life-history traits as nestling or parental survival and clutch size (Kisdi and Meszéna, 1993; Sibly and Calow, 1983). Experimental studies induced by optimal foraging and life-history theories have brought plenty of evidence for tradeoffs between traits increasing the per capita population growth rate – e.g., between resource utilization efficiencies or life-history traits (Friedman, 2020; Martin, 1995; Pyke et al., 1977).

In contrast to functional constraints, embryologists and developmental biologists emphasized the importance of developmental constraints on emerging variation

> Considerations of developmental mechanisms in evolution are essential to understand phyletic trends since developmental interactions basically define the universe of possible morphologies and impose limits on the directional action of natural selection. (Alberch, 1982:313)

Maynard Smith et al. (1985) defined developmental constraints as “*biases on the production of variant phenotypes or limitation on phenotypic variability*”. Understanding the regulatory evolution of development (Carroll et al., 2013) in an ecological context (Gilbert and Epel, 2009) joins the ecological and developmental approaches to evolution with a reinforcement of the constrained nature of emerging variation.

Stochasticity

A completely new contribution of population genetics to evolutionary theory was the discovery of the huge amount of molecular polymorphisms and the description of their stochastic dynamics (Crow and Kimura, 1970; Harris, 1966; Lewontin and Hubby, 1966). Today, the stochastic nature of population processes has become an essential object of evolutionary and ecological studies. Genetic drift and demographic stochasticity are the consequences of small population sizes, while environmental stochasticity is due to the capricious dynamics of the environmental conditions (Lande et al., 2003). Although the essential stochasticity of natural processes does not change the logical structure of the core theory, developing the mathematical theory of stochastic processes poses severe challenges. While non-trivial, especially for structured populations, it has been shown that population size in a stationary fluctuating environment tends to fluctuate around a deterministic exponential trajectory in the absence of feedbacks (Tuljapurkar, 2013). This mathematical result also supports the heuristic argument that the long-term growth rate has to be nullified by regulating feedbacks even in the presence of stochastic environmental variability and fluctuations do not limit the validity of the *Principle of Competitive Exclusion* (Barabás et al., 2012; Parvinen and Meszéna, 2009).

In the face of stochasticity and contingency, it has become crucial to give special attention to determining the temporal and spatial scales applied in each study. Transient states may last for decades (Bowen et al., 2003), and set of populations (Buri, 1956), metapopulation (Hanski, 1999), or metacommunity (Holyoak et al., 2005) are the appropriate levels of study for testing theoretical hypotheses in a variety of lab and natural systems.

Observation-based laws and derived principles

Having introduced the basic concepts, we summarize the core of the contemporary Darwinian theory of evolution –as we see it – in Table 3. The left column contains the necessary conditions to build the theory. These conditions are well supported by observations and serve as assumptions for the derivations of the theorems in the right column. We modified (C1, C4, and C6) and supplemented Lewontin’s conditions with three more conditions (C2, C3, and C5). While living organisms show a series of essential life phenomena, C1 emphasizes that besides reproduction and metabolism, living organisms are open systems that can move or disperse (Holt, 2009b). C4 claims the well-known fact that replication is prone to errors. C6 records that some replication errors affect the survival or reproduction of the organisms. Among the three supplemented conditions, C2 and C5 are necessary conditions for non-neutral diversification and maintenance of such diversity within a community. C2 is one of the many formulations of the necessity of limitedness of population size (Scheiner, 2010:304; Urry et al., 2017:1212), and C5 claims the presence of organismal constraints on emerging variation. The stochastic nature of varying external conditions is stated in C3. These conditions are unanimously accepted and do not require further explanations. However, the literature has various formulations with essentially the same meanings.

The eight theorems in the right column are based on assumptions that follow from the conditions and are supported by mathematical formulations or logical inferences. Therefore, these are the first principles of a formalized theory. These theorems are also supported by plenty of specific models – conceptual experiments - applying diverse methods from individual-based simulation to stochastic calculus and a mass of empirical results from field observations to lab experiments. Thus, these propositions are also universal rules, i.e., laws. We focus on the new features as compared to the former theories next.

Lewontin's four propositions specify the conditions under which the genetic composition of populations of replicating reproductive units changes from generation to generation, nothing more (Wilkins and Bourrat, 2022). Including the unavoidable population dynamical consequences of reproduction into the core theory, i.e., the potential for exponential growth (T1) and its limitation (T2) on the one hand, and organismic (C5) and functional constraints (T6) on the other, leads to further theorems that explain the competition-driven autonomous emergence and maintenance of diversification (T7, T8) as well as its loss (T6) within natural communities.

The *Principle of Tradeoffs* (T6) is related to the constrained and correlated nature of emerging variation (C5) and expresses that no omnipotent, immortal, and prolific Darwinian demon (Law, 1979) can exist. The truth of this law is staggeringly borne out by the current human-induced state of the Earth.

The *Principle of Divergence* (T8) directly follows from the robust coexistence principle (T7). Thus, it assumes population regulation, constrained genetic and phenotypic variations, and tradeoffs. Inevitable competition between individuals whose populations share regulating factors may maintain several reproductive units in robust coexistence by negative frequency-dependent selection and recruit new reproductive units with less similar population regulation. It may recruit a reproductive unit with different regulation but not necessarily does so as inappropriate supply rates, increased turnover of natural enemies, epistatic interactions, or other population dynamic and genetic complexities may prevent the maintenance of a newcomer depending on the specificities of each case (Abrams, 2022). Thus, the *Principle of Divergence* sets a necessary but not a sufficient condition for diversification.

Combining the *Principle of Robust Coexistence* into evolutionary studies provides tools to determine the conditions of evolutionary branching in terms of the feedbacks regulating population growth (Meszéna et al., 2005). Determination of the ecological conditions of coexistence and the diversification of ecological systems are closely related (Edwards et al., 2018); exemplified by studies of speciation (Carnicer et al., 2008; Weissing et al., 2011), community composition (Weber and Strauss, 2016) and macroevolution as well (Weber et al., 2017).

Conditions (observations, assumptions)	**Theorems (laws, principles)**
C1: Living organisms exchange matter and energy with their environment. They can grow, move, disperse, and reproduce.	T1: *Law of Exponential Growth*: A population of reproducing organisms grows or declines exponentially in lack of feedbacks on population growth.
C2: The capacity of any region to support any population is finite.	T2: *Law of Population Regulation*: Population sizes either vary between limits or the populations go extinct. The long-term growth rate (*pgr*) of an existing population is 0.
C3: Living conditions of organisms vary stochastically in space and time**.**	T3: *Principle of Stochasticity:* Stochastic changes in population size are unavoidable due to finite population size and stochastically changing external conditions.
C4: Replication is imprecise.	T4: *Principle of Variation:* Equivalent and non-equivalent gene-kinds, clonal-types, species-kinds are repeatedly emerging.
C5: Variation of organismal traits are usually not independent. Phenotypic variability is constrained.	
C6: Some replication errors affect the survival or reproduction of the organism**.**	T5: *Law of Tradeoffs:* Not all organismal traits increasing a reproductive unit's long-term per capita population growth rate can change independently.
C6 & T2	T6: *Law of Competitive Exclusion*: In a community of non-equivalent reproductive units regulated by a single

	agent or factor in the same way, one variety excludes all others.
T2 & T5	T7: *Law of Robust Coexistence*: Robust coexistence is possible in a community of non-equivalent reproductive units. The larger the difference between the coexisting reproductive units' growth regulation, the more robust their coexistence is.
T7	T8: *Law of Divergence:* In a community of non-equivalent reproductive units, a modified unit has a chance to be established if its population regulation is sufficiently different from that of the established ones.

Table 3 The core of a Darwinian theory of diversification. "C" stands for conditions, and "T" for derived theorems.

A summary

The conclusion from Lewontin's principles is universal: the genetic composition of populations must change over time in the presence of heritable variation and differential reproductive success. We can determine the direction of these changes under any set of complicated conditions by building specific population genetic models. For example, we may find that a higher temperature selects for variant A, while a lower temperature selects for variant B under a specific set of conditions. Still, having discussed Darwin's principles and a renewed set of universal observations (assumptions) and laws (principles), we may answer why we need to extend the basic set of conditions of evolutionary processes with the fact of limited carrying capacity (finiteness) of any environment and the constrained nature of emerging variations. Sooner or later, population size changes over the evolutionary process. Therefore, if we do not consider the feedback loops regulating population growth, we cannot predict the following steps of evolution. We can model microevolution based only on relative allele frequencies but not meso-evolution (Metz, 2012), as these models do not predict the change in the conditions regulating population growth, which also shapes the composition of a population. Only competition-induced selection may lead to coexistence and divergence of genes, clones, or species via changing the feedback loops. Thus, only if we consider the finiteness of the environment and competition among the fundamental assumptions it is possible to explain the necessity of exclusion or opportunity for coexistence. Switching to population densities and explicitly presenting feedback loops result in universal conclusions about the possible directions of evolution. We expect competitive exclusion between non-identical reproductive units when reproductive units have identical or very similar feedback loops, like in the case of a single, shared one-dimensional regulating variable. Non-neutral coexistence and divergence require differentiation of the feedback loops as derived in Meszéna et al. (2006). As the existing variation constrains the emerging one and tradeoffs emerge between efficiencies and life-history traits, we may expect diversity of life forms whenever life is present.

In summary, besides constraints on emerging organismal variation and tradeoffs between the effects of the changes in organismal traits on *pgr*, we propose including finiteness among the universal assumptions and population regulation at the level of first principles of evolutionary theory. Like Lewontin's conditions, they are also consequences of the very essence of life: metabolism and reproduction. Understanding the regulation of population growth is the key to understanding coexistence and the evolutionary origin of non-neutral biological diversity.

Discussion

Instead of a long and still necessarily incomplete discussion, we reflect here on the present status of theory-making in evolutionary biology and ecology besides outlining directions of the potential use of the presented theoretical framework.

> Because the investigation of population level phenomena is so organized by specific models, a contemplation of the bulk of these models quickly reveals a characteristic of 'population biology' as a science – its nonexistence. (Lewontin, 2004:7)

Unified and integrated population biology was a dream of Robert MacArthur, Richard Levins, and Richard Lewontin in the sixties and seventies (Kingsland, 1988). However, as Lewontin's dialectical bonmot expressed decades later, population biology remained disintegrated mainly because of methodological issues (Levins, 2004). Population genetics and population ecology developed independently until the sixties, and evolutionary ecology, flourishing spectacularly ever since, has inherited the highly fragmented structure of ecology and developed mainly in isolation.

Questions to be answered, methods to be applied, and models to be tested do fragment research. Enormous methodological and technical progress with high-quality standards and a focus on application-oriented problem-solving characterize the science of our time (Green et al., 2015).

The classical goals of understanding, explaining, and synthesizing knowledge about nature have become secondary to the urgent need to solve problems caused by human overpopulation and technological progress (Courchamp et al., 2015). Scientists develop complex modeling systems to solve specific problems and base the evaluation of model quality on the accuracy of their predictions or their effectiveness in helping to achieve specific goals. Philosophers and scientists have various incompatible ideas about these transformations, the structure of science, and the role of its changing elements (Rosenberg, 2012).

In this situation, no surprise that the usefulness of any quest for a general theory has been called into question: *"The era of master theories based on ruling principles and grand schemes has long past."* (Stoltzfus, 2017:6); In a similar vein, e.g., Svensson (2023:9,10) thinks that since the modern synthesis "is a research framework of *how to do science* and a *perspective* rather than a formal theory, it follows that it cannot be replaced by any new theory let alone a new paradigm,". *"All is well"*, *"genes are central,"* and phenotypic plasticity, niche construction, inclusive inheritance, and developmental bias are just four of the many *" 'add-ons' to the basic processes that produce evolutionary change: natural selection, drift, mutation, recombination, and gene flow"* (Wray et al., 2014:164). All this raises the question of the relevance and usefulness of exploring the basic principles shaping the evolutionary processes.

Sticking to this pragmatic perspective and with all due respect, we share Levins (2004)' assessment:

> Meanwhile, much of the work in population genetics has been aimed at answering the questions of population genetics in the narrow sense, such as estimating selection pressure or effective population size. The demand for precision has tended to overwhelm the criteria of realism. But a successful study of evolution requires the recognition of the complexity not only of the genotype but also of the environment and of the whole organism in its development and its physiological flux.

Upon acceptance that the "contemporary mainstream thinking" provides research frameworks that suggest vantage points and directions for developing methods, it is evident that the presented set of conditions, principles and logic assumes perspectives utterly different from those presented by the "all is well" framework.

First, the subjects of the principles are the reproducing entities which, depending on the mode of reproduction, may reproduce their alleles and their clonal or species identity – not just genes. Second, the theory aims to reveal the necessary conditions of diversification and extinction instead of determining the conditions of "evolutionary," i.e., gene frequency change. Third, feedback loops, i.e., interactions between the reproducing entities regulating their populations, provide the vantage points, not only those "basic processes" that influence allele frequencies. This inclusive framework offers solutions to the problem raised by Richard Levins' assessment: the complexity of the environment as well as of "the whole organism in its development" are necessarily in the focus when the starting question is about the feedback structure regulating population growth. Reciprocal causations (Laland et al., 2011; Mayr, 1961; Pásztor et al., 2016b; Svensson, 2018) from genes to population characteristics and back to genes via the effects of environmental factors/agents controlling population growth ultimately include the organism's behavior and "physiological flux". While the inclusive theory follows the dynamics of interacting populations, the principles about exclusion and robust coexistence (T7, T8) set conditions for the determination of the *kinds* of organisms that can maintain themselves or can coexist, moreover C5 and T5 express the assumption that developmental processes as well as environmental conditions, generically constrain the combination of organismal traits.

Changed perspectives change how to teach and communicate the evolutionary theory to the public and necessarily change the research questions to be asked and methods to be applied. The primary question is which direct or indirect interactions keep a population in check and why. How a population is regulated determines the time and spatial scales to be applied in its study. Forty years was enough to reveal the basic evolutionary mechanisms shaping the traits of the most common finch species on a tiny island (Grant and Grant, 2014); however, the finch community on the whole Galapagos archipelago has to be taken under study on longer time scale when extinctions and colonizations are frequent. Similarly, evolutionary perspectives of species maintained mainly by competition-colonization tradeoffs in metacommunities differ from species regulated by local resources or predators. The regulatory aspect also *ab ovo* requires connecting the structure, behavior, and physiology of the organisms and their population-dynamical consequences, thus requiring the integration of many different kinds of knowledge. For instance, explanations of evolutionary branching in microbial systems (Good et al., 2017; Lunzer et al., 2002) and sympatric speciation (Brodersen et al., 2018; Taylor and Friesen, 2017) require detailed knowledge of the characteristics of competition, e.g., for resources, based on the understanding genetics and organismal biology (Grosskopf et al., 2016; Pásztor, 2022).

Enforcing the regulatory aspect can be combined with any approach modeling allele or species dynamics. It is essential to make a difference between models aimed to explain and be applied to particular situations and general rules that govern their behavior. We share a theory-centered view of science (del Rio, 2008; Pásztor et al., 2016a) with many of our colleagues (Rossberg et al., 2019). We presented the core of a Darwinian theory consisting of observation-based assumptions and derived rules. These rules may provide structures for an evolutionary theory as the armature does for a statue (Pásztor et al., 2016a). Besides structuring, governing rules or laws are falsifiable by a model – a conceptual experiment - an experiment, or an observation. Laws are important as they influence the model makers' abstractions and the experimentalists' search images. The theory sets methodological problems to be solved and standards for the interpretation of models. Darwinian principles shift the focus to the explorations of feedback loops regulating population growth and the traits shaping them as they determine the opportunities for coexistence and evolution. The fact that the logical structure of Darwin's mature theory remained intact over centuries and that only its expression developed over time, reinforces our conviction that natural laws exist in our rapidly changing world and science gets closer and closer to their deep understanding.

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It contains the citations with links to the original texts.

Line 4: No matter how embarrassing it is, evolutionary biologists often express deep-rooted conflicting views on fundamental issues and the dominant processes of evolution (Laland et al., 2014; Scheiner, 2010:295; Wray et al., 2014)

"The other four fundamental principles— gradualism, variation, natural selection, and contingency—are a different story. These principles are about the mechanisms of evolution. They have been, and continue to be, the subject of sometimes vociferous debate. … The past 50 years have seen additional debates over those mechanisms and the meaning of the concepts embodied in the fundamental principles."

In: Scheiner, S. 2010. Toward a conceptual framework for biology. The Quarterly review of biology, 85:293-318. p.295

Line 48-9: … based on his taxonomic work on barnacles he did not think anymore that organisms "*vary exceedingly little*" (Darwin, 1909:81)

In: Darwin, F. (ed). 1909. *The Foundations of the Origin of Species: Two Essays Written in 1842 and 1844*. Cambridge: Cambridge University Press. Darwin Online, p.81.

Line 59-61: Darwin was as much "… *a theoretical biologist in the mechanistic tradition*" (Penny, 2009) as an experimentalist and naturalist.

Line 62-4: *"If you don't have a theory you might just as well count the stones on Brighton beach".*

In: Penny, D. (2009) Charles Darwin as a theoretical biologist in the mechanistic tradition Trends in Evolutionary Biology **1**(1): e1. p.3.

Line 64: "*awfully flat*"

In: Darwin, Francis ed. 1887. The life and letters of Charles Darwin, including an autobiographical chapter. London: John Murray. Volume 2. Darwin Online p.44.

Line 67: *Principle of Divergence* (Darwin 1872:87)

“Here, then, we see in man's productions the action of what may be called the principle of divergence, causing differences, at first barely appreciable, steadily to increase, and the breeds to diverge in character, both from each other and from their common parent.

But how, it may be asked, can any analogous principle apply in nature? I believe it can and does apply most efficiently (though it was a long time before I saw how), from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers.”

In: Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. London, Albemarle street, John Murray. Darwin Online p.87.

Line 68-71: The keystone of his theory, as Darwin called it, provided a firm solution to the problem of diversification as it is a deduction from the two pillars of his theory; the “*principle of geometrical increase”* and the “*doctrine of Malthus*” (Darwin 1872:50).

“A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year; otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them.”

In: Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. London, Albemarle street, John Murray. Darwin Online p.50.

Line 71-2: Being a keystone, it also “*… distributes the weight between the core theory and the evidence for descent*” (Kohn, 2009:87).

“Darwin chose an apt architectural image when he wrote J. D. Hooker that 'the "principle of Divergence" ... with "Natural Selection" is the key-stone of my Book' (Correspondence 7; 102). In the Origin, the fifteen-page section on divergence is placed strategically at the end of Chapter 4 on natural selection, where it distributes the weight between the core theory and the evidence for descent. Darwin portrays adaptation and the origin of species as emerging out of the entangled plenitude of mutual relations mediated by natural selection. The principle of divergence united this ecological vision with Darwin's complementary view that evolutionary history can be read in the irregular branching of the taxonomic tree of life.”

In: Kohn, D. (2009). Darwin's Keystone: The Principle of Divergence. The Cambridge Companion to the 'Origin of Species'. M. Ruse and R. J. Richards. Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, Sao Paulo, Delhi, Cambridge University Press**:** 87-108. p.87.

Line 74-5: As Provine (1985:826) noted, the neo-Darwinian or synthetic views "*differed substantively"* from Darwin's views in the *Origin*.

"Most of the current controversies about mechanisms of evolution center upon proposed revisions of the "neo-Darwinian" or "synthetic" views developed in the 1930s and 1940s and expressed most clearly in the host of publications at about the time of the Darwin Centennial of 1959. Darwin's own views actually *differed substantively* from those of neo-Darwinians in 1959."

In: Provine, W. B. (1985). Adaptation and Mechanisms of Evolution After Darwin: A Study in Persistent Controversies. The Darwinian Heritage. D. Kohn, Princeton University Press**:** 825-866. p.826.

Line 88-90: Our ecological textbook that presents general ecology based on seven Darwinian principles also incorporated The *Principle of Divergence* in relation to niche segregation (Pásztor et al. 2016b:5, 200-3).

p.4. "Darwin explained how variants become different in order to survive in each others' presence, i.e., to coexist, by the principle of divergence: '… the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers' (ibid., p.87). (Here the 'place in the polity of nature' corresponds to the modern notion of niche.)"

p.200-3: Subsection of TBE: **10.1 Diversification is an essential feature of life**

Line 141-2: They "*provide a purely mechanical basis for evolutionary change"* (Lewontin, 2010).

"The modern skeletal formulation of evolution by natural selection consists of three principles that provide a purely mechanical basis for evolutionary change, stripped of its metaphorical elements:"

In: Lewontin, R. C. (2010) "Not So Natural Selection." The New York Review of Books. May 27, 2010 issue, https://www.nybooks.com/articles/2010/05/27/not-so-natural-selection/. Seen: 02.08.2022

Line 151-7: Lewontin (2010) repeatedly argued that it is often enough to prove that a particular trait „… *confers a reproductive advantage*". One does not have to bother finding the potential causes, as there are countless of them. Evolutionary biologists should not „… *engage in idle speculation*" about adaptation as it is almost hopeless to find out what caused the advantage of one form over the other, especially in the past. Organisms construct their niches, „… *there is an infinity of ways an organism might make a living, an infinity of ways putting together the bits and pieces of the external world*" (Lewontin, 2010).

In: Lewontin, R. C. (2010) "Not So Natural Selection." The New York Review of Books. May 27, 2010 issue, https://www.nybooks.com/articles/2010/05/27/not-so-natural-selection/. Seen: 02.08.2022

Line 164-7: Lewontin (1970:1) wrote: *"... the element of competition between organisms for a resource in short supply is not integral to the argument"*.

"Thus, although Darwin came to the idea of natural selection from consideration of Malthus' essay on overpopulation, the element of competition between organisms for a resource in short supply is not integral to the argument. "

Lewontin, R. C. (1970). "The Units of Selection." Annual Review of Ecology and Systematics **1**(1): 1-18. p.1.

Line 175-7: For example, in cheiner's (2010:296) framework, these three conditions define a *subsidiary theory* of a more general theory of evolution.

In Subsection: **Subsidiary theories and models**

"Within the general theory of evolution are nested a large variety of more specific theories. As an exemplar, consider the theory of natural selection. That theory consists of the following syllogism (Darwin 1859; Endler1986):….."

Scheiner, Samuel M. 2010. "Toward a conceptual framework for biology." The Quarterly review of biology no. 85 (3):293-318. P- 296.

Line 185-6: Gause, who was called a member of "*the modern school of population students*" (Pearl, 1934:VI)

He marshals to the attack on the old problem of the consequences of the struggle for existence the ideas and the methods of the modern school of population students.

In: Pearl, R. (1934). Foreword. The struggle for existence. G. F. Gause. Baltimore, USA, The Williams & Wilkins Company. p.VI.

Line 191-4: “It seems to us that there is a great future for the Volterra method here, because it enables us not to begin the theory by the coefficient of selection but to calculate theoretically the coefficient itself starting from the process of interaction between the two species or mutations. (Gause 1934:111).”

In: Gause, G.F. (1934) The struggle for existence. Baltimore, USA, The Williams & Wilkins Company. p.111

Line 200-2: After Haeckel, who defined ecology as “*the science of the struggle for existence*” (Cooper, 2003:4-6), those formulations may be safely called ecological interpretations of Darwin’s theory that refer to the struggle for existence (competition).

In Subsection: **1.3. The science of the struggle for existence**

Cooper, Gregory J. 2003. The Science of the Struggle for Existence: On the Foundations of Ecology, Cambridge Studies in Philosophy and Biology. Cambridge: Cambridge University Press. p.4-6.

Line 218-20: According to Rosenberg, *“a claim about the mechanism of evolution”* should be “*a claim about reproducing members of any line of (reproductive) descent*” (Rosenberg 2012:172).

“In order to capture the theory of natural selection’s generality, we can’t express it as one about giraffes, or mammals, or animals, or even organisms. That is because as a general claim about the mechanism of evolution that could obtain anywhere in the universe at any time (something needed to make it a set of scientific laws), it can’t mention things that are specific to the Earth. We need to express it as a claim about reproducing members of any line of (reproductive) descent.”

In: Rosenberg, A. (2011). Philosophy of Science A Contemporary Introduction. New York and London, Routledge Taylor & Francis p.172.

Line 228-31: The system of discrete alleles at the same gene locus competing for existence within a single population of organisms is perfectly isomorphic with the system of different species of organisms competing for existence in the same habitat and ecological niche. (Hardin 1960:1296)

“*Genetics*. The application of the exclusion principle to genetics is direct and undeniable. The system of discrete alleles at the same gene locus competing for existence within a single population of organisms is perfectly isomorphic with the system of different species of organisms competing for existence in the same habitat and ecological niche.”

In: Hardin, G. (1960). "The Competitive Exclusion Principle." Science **131**: 1292-1297. p.1296.

Line 252-54: ...how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? (Darwin, 1859:61; 1872:48).

In: Darwin, C. (1859). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 1st edition London, John Murray. Darwin Online p. 61.

In: Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.48.

Line 269: *Principle of Natural Selection* (Darwin, 1872:49)

“Owing to this struggle, variations, however slight, and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals, and will generally be inherited by the offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection.”

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.49.

Line 270: *Principle of Divergence* (*ibid*:87)

“But how, it may be asked, can any analogous principle apply in nature? I believe it can and does apply most efficiently (though it was a long time before I saw how), from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers.”

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.87.

Line 270: *Principle of the Division of Labour* (*ibid*:74)

“No naturalist doubts the advantage of what has been called the "physiological division of labour;" hence we may believe that it would be advantageous to a plant to produce stamens alone in one flower or on one whole plant, and pistils alone in another flower or on another plant. In plants under culture and placed under new conditions of life, sometimes the male organs and sometimes the female organs become more or less impotent; now if we suppose this to occur in ever so slight a degree under nature, then, as pollen is already carried regularly from flower to flower, and as a more complete separation of the sexes of our plant would be advantageous on the principle of the division of labour, individuals with this tendency more and more increased, would be continually favoured or selected, until at last a complete separation of the sexes might be effected.”

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.74.

Line 271: *Rule of Similar Checks* (*ibid*: p.58-9).

“The dependency of one organic being on another, as of a parasite on its prey, lies generally between beings remote in the scale of nature. This is likewise sometimes the case with those which may be strictly said to struggle with each other for existence, as in the case of locusts and grass-feeding quadrupeds. But the struggle will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers.”

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.58-9.

Line 271-2: the corollary about the evolution of characters (*ibid*:60).

“A corollary of the highest importance may be deduced from the foregoing remarks, namely, that the structure of every organic being is related, in the most essential yet often hidden manner, to that of all the other organic beings, with which it comes into competition for food or residence, or from which it has to escape, or on which it preys.”

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.60.

Line 275-9: … Darwin regarded the principle of divergence, along with the concept of natural selection, as the "keystone" of his work. Without a keystone, of course, an arch collapses. Without an understanding of the principle of divergence, so, necessarily, does our understanding of the Origin of Species. I think the meaning of this important principle deserves our careful reconsideration. (Tammone, 1995:131)

“Given the importance of the principle of divergence to Darwin's evolutionary theory, I think we ought to avoid an unfounded complacency in our understanding of it. As I noted above, Darwin regarded the principle of divergence, along with the concept of natural selection, as the "keystone" of his work. Without a keystone, of course, an arch collapses. Without an understanding of the principle of divergence, so, necessarily, does our understanding of the Origin of Species. I think the meaning of this important principle deserves our careful reconsideration. (Tammone, 1995:131)

In: Tammone, W. (1995). "Competition, the division of labor, and Darwin's principle of divergence." Journal of the History of Biology **28**(1): 109-131. p.131.

Line 284-5: Here we reconstruct the conseptual framework (sensu Scheiner, 2010:293) of Darwin’s theory based on the close analysis of his texts and former works of the historians.

“Conceptual frameworks always exist—science is never atheoretic (Suppe 1977)—but often the theories within those frameworks are not well-articulated or explicit. Theory is important because it clarifies thinking. It forces a modicum of formality onto data interpretation, thereby refereeing scientific disputes. It reveals assumptions hidden in specific models or experiments. It shows connections among disciplines, which is especially important in guiding interdisciplinary and transdisciplinary work. It defines risky or ground-breaking research. Finally, it clarifies the central questions being addressed by a scientific enterprise.”

In: Scheiner, S. (2010). "Toward a conceptual framework for biology." The Quarterly review of biology **85**(3): 293-318. p.293.

Line 290-302: Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow from the struggle for life. Owing to this struggle, variations, however slight, and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals, and will generally be inherited by the offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, …. (Darwin 1872:48-49.)

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.48-49.

Line 313-8: The basic point of the principle of divergence is simplicity itself: the more the co-inhabitants of an area differ from each other in their ecological requirements, the less they will compete with each other; therefore natural selection will tend to favor any variation toward greater divergence. The reason for the principle's importance to Darwin is that it seemed to shed some light on the greatest of his puzzles-the nature and origin of variation and of speciation. (Mayr, 1992:344).

In: Mayr, E. (1992). "Darwin’s principle of divergence." Journal of History of Biology **25**: 343-359. p.344.

Line 321-7: Darwin’s principle of divergence derives from what he thought to be one of the most potent components of the struggle for existence. He argued that the strongest interactions would be among individuals within a population or among closely related populations or species, because these organisms have the most similar requirements. Darwin’s principle of divergence predicts that the individuals, populations or species most likely to succeed in the struggle are those that differ most from their close relatives in the way they achieve their needs for survival and reproduction. (Reznick and Ricklefs, 2009:838).

In: Reznick, D. N. and R. E. Ricklefs (2009). "Darwin's bridge between microevolution and macroevolution." Nature **457**(7231): 837-842.

Line 329-30: …the intensity of competition is determined not by the systematic likeness, but by the similarity of the demands of the competitors upon the environment. (Gause, 1934:19).

“One of these ideas is that of the "niche" (see Elton, '27, p. 63). A niche indicates what place the given species occupies in a community, i.e., what are its habits, food and mode of life. It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor. Curious examples of the existence of different niches in nearly related species have recently been obtained by A. N. Formosov ('34). He investigated the ecology of nearly related species of terns, living together in a definite region, and it appeared that their interests do not clash at all, as each species hunts in perfectly determined conditions differing from those of another. This once more confirms the thought mentioned earlier, that the intensity of competition is determined not by the systematic likeness, but by the similarity of the demands of the competitors upon the environment. Further on we shall endeavor to express all these relations in a quantitative form.”

In: Gause, G.F. (1934) The struggle for existence. Baltimore, USA, The Williams & Wilkins Company. p.19.

Line 333:. Darwin qualified his thesis as a “general rule” (Darwin 1975:201).

“Hence, I think, we may conclude, that as a general rule, the struggle for existence in its strictest yet never simple sense is most severe between the individuals of the same species, & next between the individuals of two distinct varieties, or species, or even classes if their habits are somewhat allied. In all cases, the struggle being ruled & modified by multiform relations.”

In: Darwin, C. (1975). Charles Darwin's Natural Selection; Being the Second Part of His Big Species Book written from 1856 to 1858. R. C. Stauffer. Cambridge, Cambridge University Press. Darwin Online

Line 335-6: As an effect of this principle, we seldom find closely allied species of animals or plants living together, …” (Wallace, 1889:34-35).

In: Wallace, A. R. (1889). Darwinism An exposition of the theory of natural selection with some of its applications. London, New York, MacMillen and co. p.34-35.

Line 348-52: … the struggle almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers. In the case of varieties of the same species, the struggle will generally be almost equally severe, and we sometimes see the contest soon decided.” (Darwin 1872:58-59).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.20-24.

Line 355-7: Dangers” means natural enemies here, as Darwin explained and illustrated by examples that interactions check population growth, not the weather conditions apart from extremely harsh habitats (in sink populations) (ibid:53-8).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.53-58.

Line 365-8: To keep up a mixed stock of even such extremely close varieties as the variously coloured sweet-peas, they must be each year harvested separately, and the seed then mixed in due proportion, otherwise the weaker kinds will steadily decrease in numbers and disappear. (*ibid*:59).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.59.

Line 369-71: Thus, this rule qualifies the *Principle of Natural Selection* as it identifies the condition when the "*preservation of favourable individual differences and variations, and the destruction of those which are injurious*" Darwin (1872:63), means the survival of a single variant.

"… individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest. Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions."

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.63.

In the Subsection entitled: "Illustrations of the Action of Natural Selection, or the Survival of the Fittest" Darwin's first example is the woolf types in Catskill Mountains, i.e., possible divergence. This also shows that the meaning of the expression "survival of the fittest" differed from its present-day usage for only those cases when only a single variant survives.

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.70-1.

Line 386-9: A corollary of the highest importance may be deduced from the foregoing remarks, namely, that the structure of every organic being is related, in the most essential yet often hidden manner, to that of all other organic beings, with which it comes into competition for food or residence, or from which it has to escape, or on which it preys. (Darwin 1872:60).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.60.

Line 394-404: It follows almost necessarily from what we have seen of the struggle for existence, dependent on the habits of animals & plants, that the structure of each organic being stands in most intimate relation to that of other organisms. For habit generally goes with structure, not withstanding that in most great families, a few species having the same general structure can be picked out with habits in some degree aberrant. … Obviously every living being has its constitution adapted to the climate of its home; but this seems to produce scarcely any visible difference in structure: thus in every kingdom we have a few species keeping identically the same structure under the most opposite climates—… if we run over in our mind the various structures of the commoner animals, we shall see that the manner of obtaining their prey or food & of escaping danger from other living beings is almost equally influential on their structure. (Darwin, 1975:208-9)

In: Darwin, C. (1975). Charles Darwin's Natural Selection; Being the Second Part of His Big Species Book written from 1856 to 1858. R. C. Stauffer. Cambridge, Cambridge University Press. Darwin Online p.208-9.

Line 410-6: The forms which stand in closest competition with those undergoing modification and improvement, will naturally suffer most. And we have seen in the chapter on the Struggle for Existence that it is the most closely-allied forms, —varieties of the same species, and species of the same genus or of related genera, —which, from having the same structure, constitution, and habits, generally come into the severest competition with each other; consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them." (Darwin 1872:86).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.86.

Line 418-9: How, then, does the lesser difference between varieties become augmented into the greater difference between species? - asks Darwin (*ibid*:86).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.86.

Line 421-4: from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers. (*ibid*. p.87).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.87.

Line 451-5: The *Rule of Similar Checks* and the *Principle of Divergence* should provide a basis for the causal explanation for why species "*form distinct genera and other higher groupings*". However, not only divergence but gaps between species and genera and a permanently growing and branching tree of life also had to follow from the struggle for existence (Tammone, 1995:122).

"The question for Darwin here was not simply, Why do organisms sometimes try to encroach on other stations in the economy of nature? It was also, Why do diverging organisms continue to diverge in structure generation after generation even after they have encroached on a new station? Why do they diverge so much in structure that they eventually, after tens of thousands of generations, become distinct varieties? And why, after hundreds of thousands of generations, do they diverge so much in structure that they become distinct species? And why, after even longer periods of time, do they begin to form distinct genera and other higher groupings?”

In: Tammone, W. (1995). "Competition, the division of labor, and Darwin's principle of divergence." Journal of the History of Biology **28**(1): 109-131. p.121-2.

Line 456-8: The principle of divergence united this ecological vision with Darwin's complementary view that evolutionary history can be read in the irregular branching of the taxonomic tree of life. (Kohn, 2009:87)

In: Kohn, D. (2009). Darwin’s Keystone: The Principle of Divergence. The Cambridge Companion to the 'Origin of Species'. M. Ruse and R. J. Richards. Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, Sao Paulo, Delhi, Cambridge University Press**:** 87-108. p.87.

Line 459-61: His central example of diverging slim or robust wolves hunting deer versus sheep in the Catskill mountains first appeared in his notes only in the Big Species Book (Darwin, 1975:220-1).

“In order to make it clear how I believe natural selection acts, I must beg permission to give one or two imaginary illustrations./12/Let us take the case of a wolf, which preys on various animals, securing some by craft, some by strength & some by fleetness; & let us suppose that the fleetest prey, a deer for instance, had from any change whatever increased in numbers, or other prey had decreased in numbers during that season of the year, when the wolf is hardest pressed for food; I can under such circumstances see no/<12>13/reason to doubt that the swiftest & slimmest wolves would in the long run be preserved & selected; always provided that they retained strength to master their prey at this period or some other period of the year when compelled to prey on other animals./13 v/I can see no more reason to doubt this, than that the Breeder can greatly improve the fleetness of his greyhounds by long-continued & careful selection. /13/The same process would tend to modify the deer in order to escape the wolf slowly rendered fleeter; though it might happen that some other & incompatable modification might be more important to this animal, as getting food during some other season. Even without any change in the proportional numbers of the animals on which the wolf preyed, a single cub might be born with an innate tendency either of instinct or structure leading it to pursue certain prey; nor can this be thought very improbable seeing that of our cats, one naturally takes to catch rats & another mice, & according to the excellent observer Mr. St. John one to bring home winged game, another hares & rabbits, & another to hunt on marshy ground & almost nightly to catch woodcocks & snipes, how if any innate slight change of habit or structure benefitted our wolf, it would be more likely to survive & procreate many young, than the other wolves; & some of its young would/<13>14/probably inherit the same tendency, & thus a new variety might be formed, which would either supplant or coexist with the parent form. Or again with our wolves, those inhabiting a mountainous district might readily be led chiefly to hunt different prey from those on the lowlands; & from the continued selection of the best fitted individuals in the two sites two varieties might slowly be formed, which would, cross & blend where they met, but to this subject of intercrossing we shall soon have to return; I may add that according to Mr. Pierce there are two varieties of the wolf in the Catskill Mountains in the <United States>,2 one with a light grey-hound like form which pursues deer, & the other more bulky with shorter legs & which more frequently attacks the shepherd's flocks.”

In: Darwin, C. (1975). Charles Darwin's Natural Selection; Being the Second Part of His Big Species Book written from 1856 to 1858. R. C. Stauffer. Cambridge, Cambridge University Press. Darwin Online p.220-1.

Line 467-76: Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural power of increase be allowed to act, it can succeed in increasing (the country not undergoing any change in conditions) only by its varying descendants seizing on places at present occupied by other animals; some of them, for instance, being enabled to feed on new kinds of prey, either dead or alive; some inhabiting new stations, climbing trees, frequenting water, and some perhaps becoming less carnivorous. The more diversified in habits and structure the descendants of our carnivorous animals become, the more places they will be enabled to occupy. What applies to one animal will apply throughout all time to all animals—that is, if they vary—for otherwise natural selection can effect nothing. (Darwin, 1872:87-8).

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.87-8.

Line 482-5: Pearce showed that the meaning of the metaphor changed over history from “*Linnaeus’ theologically planned economy”* to Lyell and Darwin, for whom *„the economy of nature is dynamic and subject to infinitely complex interactions”.*

Thus for Darwin, as for Lyell, the economy of nature is dynamic and subject to infinitely complex interactions – a stark contrast with Linnaeus’ theologically planned economy.

In: Pearce (2010). "“A Great Complication of Circumstances”–Darwin and the Economy of Nature." Journal of the History of Biology **43**(3): 493-528. p.518.

Line 490-5: The reason why this kind of struggle goes on is apparent if we consider that the allied species fill nearly the same place in the economy of nature. They require nearly the same kind of food, are exposed to the same enemies and the same dangers. Hence, if one has ever so slight an advantage over the other in procuring food or in avoiding danger, in its rapidity of multiplication or its tenacity of life, it will increase more rapidly, and by that very fact will cause the other to decrease and often become altogether extinct. (Wallace, 1889:34)

In: Wallace, A. R. (1889). Darwinism An exposition of the theory of natural selection with some of its applications. London, New York, MacMillen and co. p.34.

Line 502-8: The advantage of diversification of structure in the inhabitants of the same region is, in fact, the same as that of the physiological division of labor in the organs of the same individual body—a subject so well elucidated by Milne Edwards. No physiologist doubts that a stomach by being adapted to digest vegetable matter alone, or flesh alone, draws most nutriment from these substances. So in the general economy of any land, the more widely and perfectly the animals and plants are diversified for different habits of life, so will a greater number of individuals be capable of supporting themselves. (Darwin 1872:89-90)

In:Darwin, C. (1872). The Origin of Species by means of natural selection, or the preservation of favoured species in the struggle for life. 6th edition London, Albemarle street, John Murray. Darwin Online p.89-90.

Line 584-8: As Vellend (2010:188) explained in his conceptual synthesis of community ecology

The species identity is a categorical phenotype, assumed to have perfect heritability, except when speciation occurs, after which new species identities are assigned (just as mutation changes the identity of an allele).

In: Vellend, M. (2010). "Conceptual synthesis in community ecology." Quarterly Review of Biology **85**(2): 183-206. p.188.

Line: 703-5 . Frequency-dependent *pgr* of reproductive units means frequency (abundance)-dependent fitness and selection also among species within a community (Pásztor et al., 2016:170-8; Vellend, 2010)

Frequency- or density-dependent selection is central to the vast majority of theoretical models with species interactions in community ecology.

In: Vellend, M. (2010). "Conceptual synthesis in community ecology." Quarterly Review of Biology **85**(2): 183-206. p.188.

Line 793-6: Considerations of developmental mechanisms in evolution are essential to understand phyletic trends since developmental interactions basically define the universe of possible morphologies and impose limits on the directional action of natural selection. (Alberch, 1982).

In: Alberch, Pere. 1982. "Developmental constraints in evolutionary processes." In Evolution and development, 313-332. Springer. p. 313

Line 797-8: Maynard Smith et al. (1985) defined developmental constraints as "*biases on the production of variant phenotypes or limitation on phenotypic variability*".

"Developmental constraints (defined as biases on the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system) undoubtedly play a significant role in evolution. Yet there is little agreement on their importance as compared with selection, drift, and other such factors in shaping evolutionary history."

In: Maynard Smith, J. , R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. "Developmental Constraints and Evolution: A Perspective from the Mountain Lake Conference on Development and Evolution." Quarterly Review of Biology no. 60 (3):265-287.

Line 916-8: Because the investigation of population level phenomena is so organized by specific models, a contemplation of the bulk of these models quickly reveals a characteristic of 'population biology' as a science – its nonexistence. (Lewontin, 2004:7)

In: Lewontin, R. C. 2004. "Building a science of population biology." In The evolution of population biology, edited by Rama Shankar Singh and Marcy K. Uyenoyama, 7-20. Cambridge: Cambridge University Press. p. 7.

Line 937-9: In this situation, no surprise that the usefulness of any quest for a general theory has been called into question: *"The era of master theories based on ruling principles and grand schemes has long past."* (Stoltzfus, 2017)

"The era of master theories based on ruling principles and grand schemes is long past. The OMS was the last such theory. There will not be another."

In: Stoltzfus, A. 2017. Why we don't want another "Synthesis". Biology Direct, 12:1-12. p.6

Line 939-41: Svensson (2023) thinks that since the modern synthesis "is a research framework of *how to do science* and a *perspective* rather than a formal theory, it follows that it cannot be replaced by any new theory let alone a new paradigm,".

"Labelling the MS as a "theory" is, however, misleading, as it was rather a loose conceptual framework of *how to do science* than a formal theory (Cain 2009). "

"Since the MS is a research framework of *how to do science* and a *perspective* rather than a formal theory, it follows that it cannot be replaced by any new theory let alone a new paradigm, which has even been admitted by one of the leading critics of contemporary evolutionary biology; Massimo Pigliucci (Pigliucci and Finkelman 2014)."

In: Svensson, E. 2023. The structure of evolutionary theory: beyond Neo-Darwinism, Neo-Lamarckism and biased historical narratives about the Modern Synthesis. In T. E. Dickins and J. A. Dickins (eds.), Evolutionary Biology: Contemporary and Historical Refections upon Core Theory: Springer Nature. Preprint p.9, 10

Line 942-5: “All is well”, “genes are central,” and phenotypic plasticity, niche construction, inclusive inheritance, and developmental bias are just four of the many “ ‘add-ons’ to the basic processes that produce evolutionary change: natural selection, drift, mutation, recombination, and gene flow” (Wray et al., 2014).

“All four phenomena that Laland and colleagues promote are ‘add-ons’ to the basic processes that produce evolutionary change: natural selection, drift, mutation, recombination and gene flow. None of these additions is essential for evolution, but they can alter the process under certain circumstances. For this reason they are eminently worthy of study.”

In: Wray, G. A., H. E. Hoekstra, D. J. Futuyma, R. E. Lenski, T. F. C. Mackay, D. Schluter, and J. E. Strassmann. 2014. Does evolutionary theory need a rethink? - COUNTERPOINT No, all is well. *Nature*, 514:161-+. p:164

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Laland, K., T. Uller, M. Feldman, K. Sterelny, G. B. Muller, A. Moczek, E. Jablonka, and J. Odling-Smee. 2014. Does evolutionary theory need a rethink? - POINT Yes, urgently. *Nature*, 514:161-164.

Lewontin, R. C. 2004. Building a science of population biology. In R. S. Singh and M. K. Uyenoyama (eds.), *The evolution of population biology*, pp. 7-20. Cambridge: Cambridge University Press.

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Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert. 1985. Developmental Constraints and Evolution: A Perspective from the Mountain Lake Conference on Development and Evolution. *Quarterly Review of Biology*, 60:265-287.

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