Stable laws in a changing world

The explanatory structure of evolutionary theories over the centuries

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Content

Abstract

Successful fundamental theories are built on quantifiable principles. This paper shows that Darwin’s inclusive theory is built on such principles and follows their rocky road into the 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 Similarity), and Divergence are mere deductions from these conditions. At present, the system dynamic theory of robust coexistence, the theory of adaptive dynamics, and the extended theory of evolution all assume Darwin’s inclusive set of principles as essentials. While Lewontin's conditions for evolution by natural selection do not provide a sufficient basis to predict the outcome of evolution, 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.

Introduction

No matter how embarrassing it is, evolutionary biologists often express deep-rooted conflicting views on fundamental issues and the dominant processes of evolution (Scheiner 2010, Laland et al. 2014, 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, Santos, and Szathmáry 2017)? The answers to such 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 key assumptions and inferences.

According to historians, evolutionary biology has got a 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 this *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. In the second part of the last century, however, new conceptual approaches and research lines emerged. 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 differentiations, more and more theoretical evolutionary biologists started to model evolutionary processes in *ecological contexts*. The optimality and game-theoretical (ESS) models of evolutionary biology (Day 2005) put aside the problems associated with sexual reproduction and focused on the constraints on *trait evolution* rather than on 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, Christiansen, and Law 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 the context of 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 regulations 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 unanimously 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. The consensus says, Darwin gradually changed his views on three key points between 1846 and 1854 (Schweber 1985): based on his taxonomic work on barnacles he did not think anymore 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 and 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 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 interspecific 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 as "… *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 2009a). 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 the analyses of historians, it was the quest for a mechanistic theory explaining the diversification of life by 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 theory "*differed substantively"* from Darwin's theory presented 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 (Tammone 1995, Kohn 2009) 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 exactly is what the *Principle of Divergence* and Darwin's second theory expect.

Evolution by natural selection requires variation, heredity, and differential reproduction or survival. All of us educated in biology have learned Lewontin’s conditions. This paper argues that this set of conditions becomes complete only with the inclusion of 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 conditions of diversification and explains a broader range of phenomena from first principles than a theory that restricts its scope to the determination of the conditions of natural selection. Moreover**,** we demonstrate that the principles of this theory were developed and consistently presented by Darwin himself and can be expressed in current terms of theoretical biology. We think that the stability of the basic conditions (assumption) and laws (first principles) of this evolutionary theory over centuries may reflect natural laws.

In support of our proposition, we provide both 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 neo-Darwinian synthesis (Lewontin 1970, 2010) and the ecological interpretations of Darwin’s theory (Elton 1926, 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 the often overlooked system dynamical nature of his theory on the origin of species. This historical analysis based on Darwin’s texts draws on the works of Alfred Russell Wallace and several historians of science and goes one step further: it reveals the connections between the checks on population growth and divergence by presenting the nature of the close relationship of the *Principle of Divergence* and the *Rule of Similarity*. 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 integrates 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 occurs. 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). John Endler (1986) expressed the relation between allele frequency change within or between generations and the three conditions of variation, inheritance, and fitness differences as a syllogism.

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

Table 1 The four conditions of evolution by natural selection (Lewontin 2010, 1970)

Lewontin’s principles are not only observation-based and metaphor-free but also 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 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). 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 they mold themselves.

Lewontin’s principles do not refer to the population dynamical aspects of Darwin’s theory either; evolution is abstracted away from population regulation in this formulation wittingly. As Lewontin (1970:1) wrote: *“... 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). It is not essential to include population density and density-dependent population growth into the equations for modeling change in the relative frequencies of alleles. Density- and frequency-dependent genotypic selection are complications and not essential evolutionary processes within this 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 marshal 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:

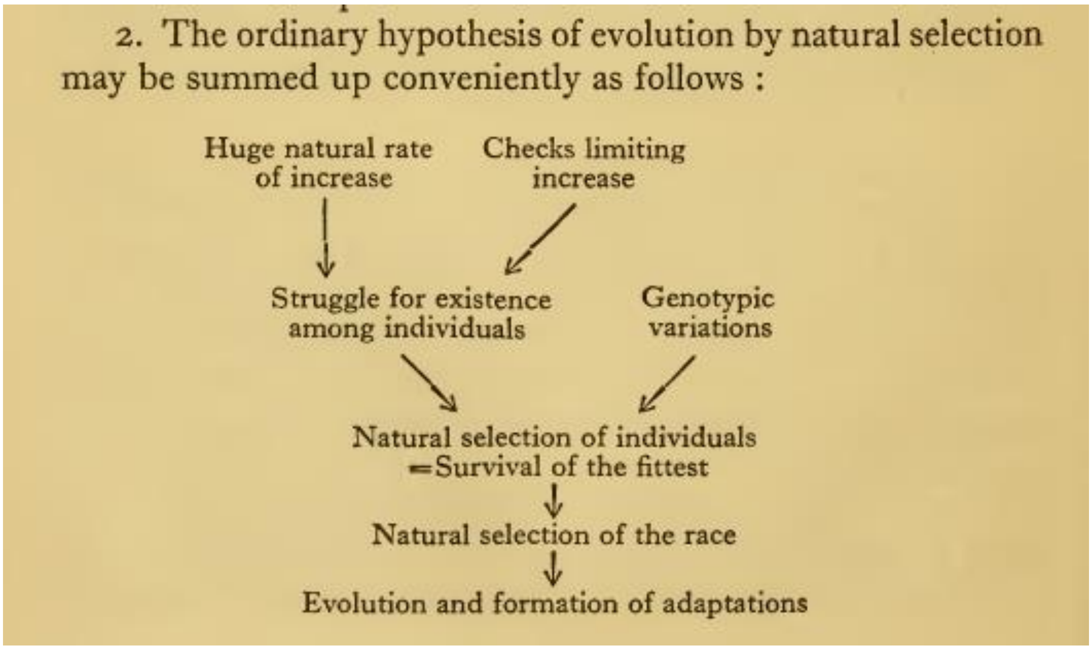
> It seems to us that there is a great future for the Volterra method here, because it enables us not to begin the theory by the coefficient of selection but to calculate theoretically the coefficient itself starting from the process of interaction between the two species or mutations. (Gause 1934:111).

Gause's insight and Kostitzin's works have 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 (Roughgarden 1979, MacArthur 1961, MacArthur 1962, Christiansen and Fenchel 1977).

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 for illustration of 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 both to 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 :

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, and 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 (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. Yet 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 variations in the physical environmental conditions (e.g. geomorphology, climatic conditions, chemical composition), and geographic isolation of populations are essential to explain the diversification of species in the context of the modern synthesis (Mayr 1963) as well as of the ecological theories of evolution of 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? Is diversification accidental or essential character of reproducing populations? - expressing the dilemma differently. 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 logically coherent 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 isolations. Darwin wanted to understand the divergence of forms in the context of their relations.

Darwin`s *“Big Species Book*” (Darwin 1975) prepared from 1854 September to 1858 June reflects the major changes in his thinking about 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. Correspondingly, he argued that evolution is favored in large populations of large, open areas rather than small isolated islands. Competition for food or space and against natural enemies instead of climate determine the geographic distribution of species and lead to extinctions (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 abundances had become a *logical necessity* for Darwin. The explanation relied on four principles: 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 Similarity* (*ibid*: 58-9).

The importance of the *Principle of Divergence* for 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, reconsideration is not an easy task as the formulation of 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), tree of life (Tammone 1995, Kohn 2009), 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.

When we reconsider Darwin's core theory, we should be aware of some difficulties. 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, 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 Similarity

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 in response to Elton's critics 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, there is a consensus that the *Principle of Divergence* relies on the idea that the strength of competition increases with the similarity of requirements. Darwin himself 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 according to Darwin. His texts show that he had a clear notion of the nature 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 followings.

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

> … 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 (sink populations) (*ibid*:53-8). He related the strength of competition to the regulating factors (agents: predators, preys, 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 Similarity*” 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

Darwin invoked several examples like the sweet-pea one in support of the *Rule of Similarity*. However, he used different examples and another formulation of the rule when he introduced the *Principle of Divergence* in the fourth chapter of the *Origin*. The divergence principle was designed 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 characters*. 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 listed in this claim, i.e., food, residence, predators, and preys, are the same ones listed in the *Rule of Similarity*; district, food, and dangers. In the "*Big Species Book*", he gave a detailed explanation of this conclusion:

> 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, according to this corollary, the structural traits of the organisms are determined by those factors or agents that they may compete for or against, i.e., place, food, and enemies.

Darwin also linked the *Rule* of *Similarity* and the *Principle of Divergence* explicitly in the fourth chapter of the *Origin* by repeating the 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 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 originates

> 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 number*" 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".*

Building a close link between the two keystones was the final step of a long process of theory construction, which Darwin confirmed by field experiments in 1855-6, according to Kohn (2009). These experiments supported Darwin's conclusion that diversity of structure means more life as it allows the varieties or species to consume different resources and escape different dangers, therefore "to increase in numbers" in presence of each other.

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

The *Rule* of *Similarity* 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's 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 actual variation of wolf types, episodes of their life, and the potential long-term consequence of selection: the evolution of two diverged forms differing in their structure, habit, and characteristic prey. As a general explanation of the principle, he supplemented the example of the Catskill wolves with an analogous, hypothetical one. It 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 Similarity*. 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, not like the *Rule* of *Similarity*, 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".* All of 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:

> 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 (Tammone 1995, Ghiselin 1999, Pearce 2010). Darwin presented it by analogy with Milne-Edwards'principle of the division of physiological labour, which brought an analogy between the organs in a body and human workers in a factory (Pearce 2010). Darwin's explanation went like this:

> 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 improvement, and it makes it possible “to increase in numbers” and to 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 favoring 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 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 either 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, which is checked either 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 that there are 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 Similarity*). 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 of historians of science. The new features of the present reconstruction of Darwin's core theory compared to the historians' interpretations reveal its population dynamical aspects and clarify the logical relation between the *Principle of Natural Selection*, the *Rule of Similarity,* and the *Principle of Competitive Exclusion.* Darwin's examples and explanations clearly show that he considered interactions 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 and 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 of them is stretching out for the complete branching tree of life as Darwin's theory has done. The explanation of inherent diversification was lost in the twentieth century.

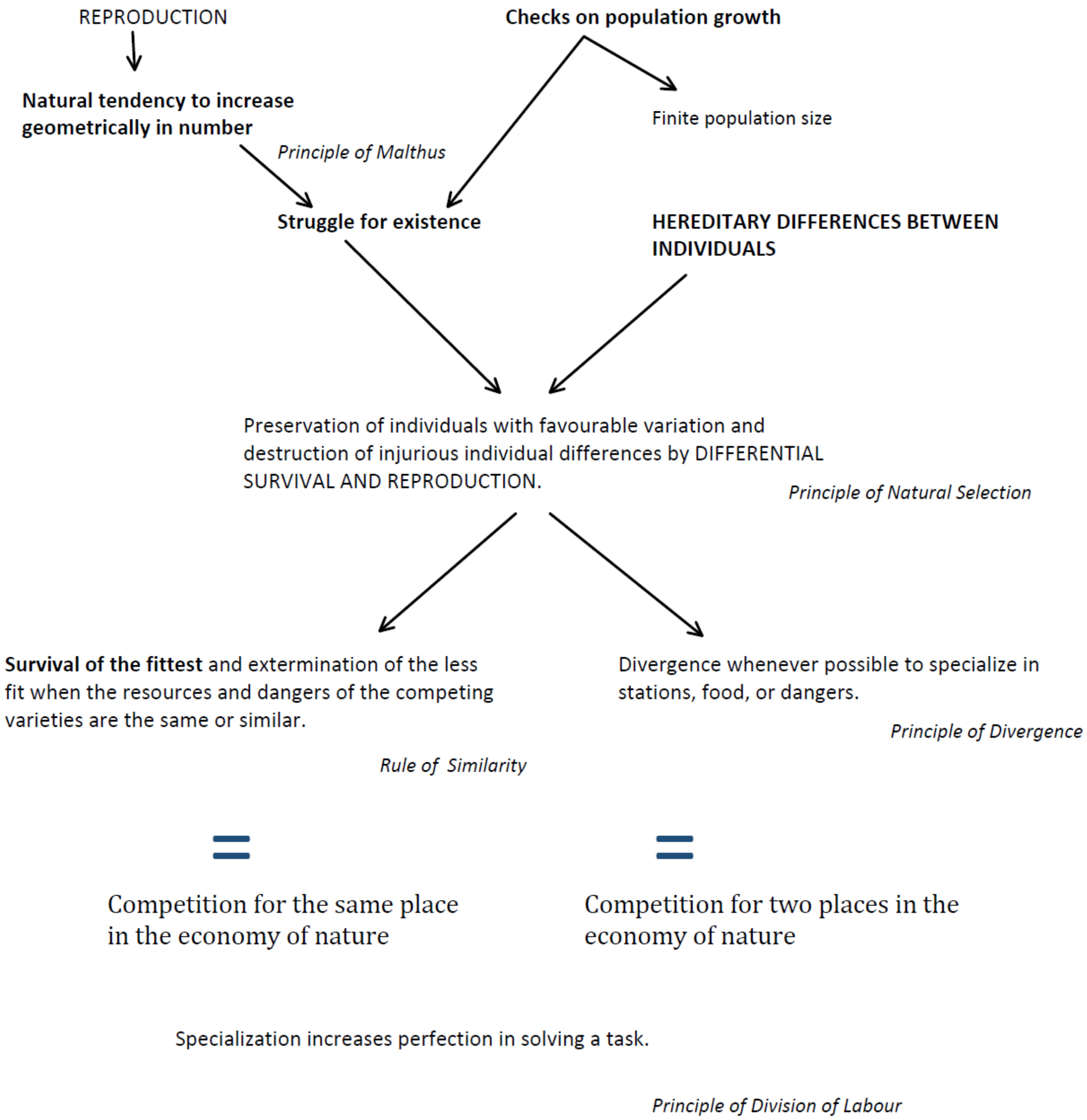


Figure 2 Framework of Darwin's core theory using his expressions. The names of the principles are in italics. Elements in agreement with Lewontin's framework are in capital letters; those that coincide with Elton's scheme are bold. Arrows denote inferences. (e.g., Because of reproduction, there is a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

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

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 theory of coexistence allow us to free Darwin's principles from metaphors and back them up with models and mathematical theory. To establish the common principles of the ecological and genetic theories of evolution, it is necessary to define their common objects and state variables and to discuss the contemporary notions of reproductive units, population dynamic fitness, feedbacks, frequency dependence, and tradeoffs.

Reproductive units

The capability of 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). Clonal and sexual reproduction 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.

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 besides genes. Selective sweeps of 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. As reproductive units with higher long-term per capita population growth rates, *pgr*s, (Sibly, Hone, and Clutton-Brock 2002, Pásztor et al. 2016b:42-3) increase in numbers relative to the ones with lower ones, *pgr*s of reproductive units are used in place of fitness. In presence of different reproductive units, their relative frequencies change according to the differences between their *pgr*s, and 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 (Lande 1982, Charlesworth 1994, McPeek and Gomulkiewicz 2005, Metz 2008, Lande, Engen, and Sæther 2009, Brown 2016a, Pásztor et al. 2016b, McPeek 2019). Defining fitness as the population growth rate is just a generalization of any definition based on survival and reproduction, as population growth is determined by and can be calculated from birth and death rates in any stage-structured population, at least in principle (Caswell 2001, Metz, Nisbet, and Geritz 1992).

As Sober (2014) discussed from several standpoints, fitness is *not* an individual trait that *leads to* certain 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 certain 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 effect 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 models of population genetics, 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 at 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, as, e.g., competitive experiments between species exemplify (Pásztor et. al. 2016:121-31). On the other hand, revealing genomic patterns makes it also possible to estimate the selection intensity on haplotypes directly, without estimating the 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 (Mueller-Dombois and Ellenberg 2003, Andrewartha and Birch 1954) or requirement (sensitivity) niche (Chase and Leibold 2003, Meszéna et al. 2006, Holt 2009b). It is also a basic observation and considered to be a first principle of biochemistry (Nelson and Cox 2017) that living organisms are open systems. They constantly influence their environments through their metabolic activity and also 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 also deteriorate or facilitate each other's existence for example, when they have an effect on their surroundings that decreases or increases the chances of other organisms’ survival or reproduction.

Some of these interactions create feedback loops including the *pgr*s and the densities of the populations. 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 (Turchin 2003, Sibly, Hone, and Clutton-Brock 2002). 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 control of population growth is realized by the organisms' impacts on and sensitivity to the regulating variables of their populations (Figure 3).

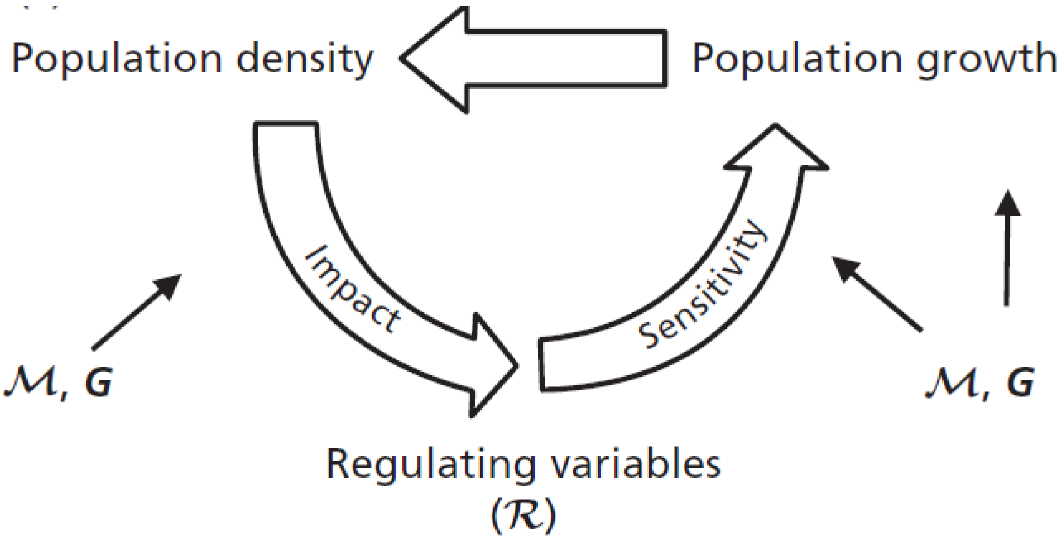


Figure 3 Living organisms depend on and affect their environment. Their populations are regulated by negative feedbacks through the changing quantities of external regulating variables (R) and this feedback loop is modified by the quality of environmental conditions (M, modifying variables) and genetic effects (G) (Meszéna et al. 2006, Pásztor et al. 2016b:14-6).

The *Principle of Competitive Exclusion* that closely follows from the limited nature of any population growth seems to be trivial for many as it had been discussed by Hardin (1960) 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 (Chesson 1991, Chesson and Huntly 1997, Meszéna et al. 2006, Fox 2013, Barabás, D'Andrea, and Stump 2018). There are plenty of models demonstrating the validity of the principle in cases where the competing units share a single 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, Mylius, and Diekmann (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-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, Levine, and Gilbert 2019), as well as in terms of the regulating factors or agents and the characteristics of the controlling feedback loops in equilibrium (Tilman 1982, Meszéna et al. 2006, Leibold 1995, Barabás 2017). 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 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 (Meszéna et al. 2006, Barabás et al. 2014).

Besides the stability of 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, in case their fitness decreases with their frequency. However, their coexistence will be sensitive to any changes in the circumstances influencing their fitness functions (Barabás et al. 2014). It was shown, for linear and non-linear feedbacks analytically in a model-independent way, 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 (McPeek 2019, Germain et al. 2018), 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, Barabás, and Meszéna 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 (Clarke 1979, Antonovics and Kareiva 1988, Christiansen 1988, Rosenzweig 1978, Mallet 2012). However, in the classical population genetic framework as Mallet (2012) put it

> Models of frequency-dependent selection are normally developed without any explicit demographic rationale. Mallet (2012:649)

In contrast, frequency dependence is an essential, inseparable property of the theory of adaptive dynamics (Brown 2016b, Metz 2012). Its form 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, Metz, and Kaitala 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 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).

The integration of the coexistence problem into evolutionary ecology and the increasing importance of ecologically induced frequency-dependence in evolutionary genetics have brought significant changes towards the integration of 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 as a result of 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 analyzed systematically the potential consequences of tradeoffs among such life-history traits as nestling or parental survival and clutch size (Sibly and Calow 1983, Kisdi and Meszéna 1993). 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, Pulliam, and Charnov 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, Grenier, and Weatherbee 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 (Harris 1966, Lewontin and Hubby 1966, Crow and Kimura 1970). 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, Engen, and Sæther 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 presence of stochastic environmental variability and fluctuations do not limit the validity of the *Principle of Competitive Exclusion* (Barabás, Meszéna, and Ostling 2012, Parvinen and Meszéna 2009).

In face of stochasticity and contingency, it has become especially important to give special attention to the determination of the temporal and spatial scales of studies. Transient states may last for decades (Bowen, McMillan, and Mohn 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 summarized 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 given in the right column. Lewontin’s conditions are modified (C1, C4, and C6) and supplemented 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 2009a). C4 claims the well-known fact that self-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 (Urry et al. 2017:1212, Scheiner 2010:304), 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, they have various formulations in the literature 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 also supported by a mass of various 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 one generation to the next, 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 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. Inevitable competition between individuals whose populations share regulating factors may maintain several reproductive units in robust coexistence by negative frequency-dependent selection and may recruit new reproductive units with less similar population regulation. 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 (Weissing, Edelaar, and Van Doorn 2011, Carnicer, Abrams, and Jordano 2008), 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 exponentially in lack of feedbacks.
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 must be exactly 0.
C3: Living conditions of organisms vary stochastically in space and time**.**	T3: *Principle of Stochasticity:* Stochastic changes in population sizes are unavoidable due to finite population size and stochastically changing external conditions.
C4: Self-replication is imprecise.	T4: *Principle of Variation:* Equivalent and non-equivalent gene-kinds, clonal-types, species-kinds are emerging repeatedly.
C5: Variations of organismal traits are usually not independent. Phenotypic variability is constrained.	
C6: Some replication errors affect survival or reproduction of the organism**.**	T5: *Law of Tradeoffs:* Not all organismal traits increasing the long-term per capita population growth rate of a reproductive unit 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 common, 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 competing 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 one 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 higher temperature selects for variant A, while 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 shape the composition of a population. It is only competition-induced selection that may lead to coexistence and divergence via changing the feedback loops within a community. Thus, only if we consider the finiteness of the environment and competition among the fundamental assumptions it is possible to explain exclusion or coexistence. Switching to population densities and modeling feedback loops result in universal conclusions about the direction of evolution. We expect competitive exclusion between non-identical reproductive units in the case of a single, shared regulating variable. Non-neutral coexistence and divergence require differentiation of the feedback loops. 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 variation and tradeoffs between organismal traits, 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

Needs and opportunities for unification and integration

> 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)

Since Darwin's work, population biological principles have formed the basis of the studies of evolutionary processes. 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. 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.

Unification and integration (sensu Odenbaugh, 2011) are possible in formerly isolated research areas. Conceptual unification is based on principles as principles define families of models. Large model families associated with the *Principle of Exponential Growth* or the *Principle of Competitive Exclusion* illustrate that theories may be challenged and potentially refuted not only because of empirical observations but by any member of a model family that leads to a contradiction with the family-defining principle. Models constructed for falsifying the narrowly defined versions of the competitive exclusion principle provide examples of this practice (Armstrong and McGehee 1980).

A general complaint against the mainstream evolutionary theory is that it has a gene-centric view and “has come to *focus almost exclusively on genetic inheritance and processes that change gene frequencies*” (Laland et al. 2014:161). It may seem that the theory presented here as inclusive, is rather like the standard one, except that it follows the dynamics of reproductive units not only of genes. While it is true that most of the principles concern the dynamics of interacting reproductive units, the principles about exclusion and robust coexistence (T7, T8) set conditions for the determination of the *kinds* of reproductive units that can maintain themselves or can coexist, moreover C5 and T5 assume that the combination of traits associated with a reproductive unit is restricted by developmental processes as well as by environmental conditions.

Besides *unifying* ecological and genetic approaches, exploration of the feedback loops may raise the *integration* of biological research to a higher level. Reciprocal causations from genes to population characteristics and back to genes (Mayr 1961, Laland et al. 2011, Pásztor et al. 2016b, Svensson 2018) include a series of organizational levels often studied in isolation at present. Following Darwin's logic closely leads to a dynamic systems theory of evolution that incorporates both biotic and abiotic environmental feedbacks that regulate population growth. For instance, explanations of evolutionary branching in microbial systems (Good et al. 2017, Lunzer et al. 2002) and sympatric speciation (Taylor and Friesen 2017, Brodersen, Post, and Seehausen 2018) also require detailed knowledge of the characteristics of competition e.g., resources besides understanding genetics and organismal biology (Grosskopf et al. 2016).

Theory, models, and pragmatism

The science of our time can be characterized by enormous methodological, and technical progress with high standards of quality and a focus on application-oriented problem-solving. 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). Complex modeling systems are developed to solve specific problems, and their quality is evaluated based 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 various elements (Rosenberg 2012).

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 like the armature does for a stature (Pásztor et al. 2016a). Hundreds of models obey these rules, each differing in what terms they include (e.g., whether a population has self-limitation or not, besides being limited by resources), in the forms of their ingredient functions (e.g., the form of resource-dependence), and their parameter values (e.g., particular values for the resource supply rate). Principles define their model families. Models associated with the *Principle of Exponential Growth* do not include feedbacks, the ones related to the *Principle of Competitive Exclusion*, each of them has a single, simple regulating feedback, etc. Besides structuring, this theory provides governing rules, or laws that are falsifiable either by a model – conceptual experiment -, an experiment, or an observation. Laws are important as they influence the abstractions of the model makers and the search images of the experimentalists. The theory sets methodological problems to be solved (e.g., identification of the components of feedback loops) and standards for the interpretation of models. Darwinian principles may also shift the focus to the explorations of feedbacks regulating population growth and to the traits shaping them as they may determine the opportunities not only for coexistence but also for evolution. The fact that the logical structure of Darwin’s mature theory remained intact over centuries and 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 understanding them.

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