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Natural Selection



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Definition

Differences in the propagation of genes in a population as a result of survival and reproduction of organisms carrying those genes.

Introduction

Charles Darwin described natural selection in private essays in 1842 and especially 1844 (Darwin 1909; Glik and Kohn 1996, pp. 90–96). He then drafted a large manuscript on natural selection, which he left unfinished. It was subsequently overlooked until recently (Darwin 1975). Eventually in 1858, the Linnean Society published a version of his 1844 essay in conjunction with a communication from Alfred Russell Wallace. Wallace presented some related ideas, but not natural selection as we now understand it (Bulmer 2005). Soon afterward there appeared *On the Origin of Species / By Means of Natural Selection, / or the / Preservation of Favoured Races in the Struggle for Life* (Darwin 1859), which developed the concept in detail.

Introducing natural selection on the first few pages, Darwin emphasized the importance of variation among individuals, in particular hereditary variation, and a “struggle for existence,” in other words, competition, because “many more individuals of each species are born than can possibly survive”. He thus reasoned, “It follows that any being, if it vary however slightly in any manner profitable to itself ... will have a better chance of surviving and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form.” He also recognized that natural selection is a means of the “coadaptation of organic beings to each other and to the physical conditions of life” (Darwin 1859, pp. 4–5).

Inherited differences in reproduction, as well as survival, can also lead to natural selection. Darwin emphasized this possibility when he proposed that differences in attracting mates or competing for them could lead to the special case of sexual selection. Attraction of mates proved to be especially controversial for Darwin’s successors. It implied the evolution of behavior, not just morphology. The idea that natural selection might produce preferences for mates, particularly by females, was inconceivable to most scientists in the late nineteenth century.

Darwin’s original theory thus included all of the essential elements of our current understanding of natural selection (see, for instance, Maynard Smith 1998). Natural selection is a mechanism of evolutionary adaptation that results

from a combination of heritable variation among individuals and differences in their survival or reproduction correlated with this variation. Natural selection does not require individuals to change, but it does require new variants to arise occasionally through reproduction. Natural selection requires more than individual differences in survival and reproduction. It also requires heritable variation in these differences. Darwin's presentation of natural selection included these elements but left many uncertainties, largely because the sciences of genetics and ecology had yet to come.

Basic Issues

When Darwin proposed natural selection, no one understood the mechanisms of heredity. Darwin himself conducted extensive experimental investigations of heredity and selection in domestic pigeons, but he was disturbed by his results. Offspring of differing parents often either combined the parental features or had intermediate features. Inheritance in this way, by blending of parental traits, could not produce adaptation by natural selection. Populations would instead converge on an overall average and then no longer change. Nevertheless it was apparent that pigeons did sometimes inherit parental features without complete blending. Within 50 years, examples of particulate inheritance and its infrequent mutations had been thoroughly verified. The inchoate field of genetics had provided Darwin's theory with the requisite mechanisms for heredity and variation, in the form of genes, each with variants (alleles).

Furthermore, it became clear that all steps in the process of natural selection – differences in survival and reproduction, heritabilities, and rates of mutation – were measurable and thus open to mathematical analysis. Within the first decades of the twentieth century, the mathematical theory of evolution by natural selection had established its basic principles. Evolution, that is, a change in the frequencies of alleles in a population of organisms, depends quantitatively on a balance between selection, mutation, and migration

between populations, as well as the inherent randomness in each of these three processes. Selection is included in equations for changes in allele frequencies by adding a coefficient to adjust the relative survival or reproduction of each allele. Random changes in allele frequencies become more pronounced in smaller populations. Within small populations, rare alleles are more likely to be lost, and one allele is likely to become “fixed” (universal), so random genetic variation among individuals is reduced. On the other hand, random genetic variation among small populations is enhanced.

Concurrently with the theoretical advances, experimental studies in laboratories and quantitative studies of populations in natural conditions confirmed all of these processes (Dobzhansky 1937). It was found that individuals in a population often differ in survival or reproductive success, these differences are often heritable, and genetic variation depends on the sizes of populations. Hoekstra et al. (2001) and Kingsolver et al. (2001) provide reviews of the prevalence of selection in natural populations.

The theoretical study of natural selection and evolution has in recent decades developed great sophistication in exploring the manifold complexities of population size and structure, mating systems, social interactions, migration, and isolation. Empirical studies continue to document the relevant processes. These studies, especially in natural conditions, face challenges in verifying small effects of selection and complex contingencies, in conjunction with randomness in finite populations. These effects are just the sort that theoretical investigations tend to explore.

Despite these theoretical and empirical advances, natural selection still has its perplexities and confusions. Natural selection, those who study it agree, results from the correlated consequences of individual variation, heredity, reproduction, survival, and competition and produces adapted change in the composition of a population. In various contexts, these components have raised many contentious issues. Is natural selection the result or the cause of adaptations? What kinds of variation and heredity are affected by natural selection? How do survival and

reproduction interact? What about cooperation as well as competition? Even more important, is natural selection fundamentally misleading? On the one hand, is it so simple that it reduces to a tautology and explains nothing? On the other hand, is there enough complexity to explain the emergence of cooperation, culture, language? Is it even specifically a biological process?

First, a clear definition is needed. Natural selection, along with mutation, migration, and drift (randomness), produces evolution. Evolution is a change in the genetic structure of a population of organisms. In the simplest case, it is a change in the frequencies of alleles in the population. Natural selection then occurs when individuals differ in their survival or reproduction in ways associated with differences in their alleles. It is important to point out that natural selection does not result merely from differences in survival or reproduction of individuals. It also requires heritability of those differences. Natural selection is thus a change in the frequencies of alleles in a population as a result of differences in the survival and reproduction of individuals that carry those alleles. It is a matter of arithmetic: in any population, genetic variants spread when they leave more copies in successive generations.

Such a definition resolves one basic issue above. Natural selection is not tautological. It is not survival of those that survive. It both results from adaptation (of individuals) and produces adaptation (of populations). The general principle is indeed simple and self-evident. If individuals with particular features survive and reproduce better than others (call these individuals adapted) and if reproduction preserves features of the original, with occasional variation, then a population will accumulate adapted individuals. This concatenation of simple arithmetical steps is unarguable.

Heritable Differences

The mechanisms of heredity and variation have become progressively clearer and their complexities better understood. Within 50 years after the *Origin of Species*, the particulate inheritance of discrete features of plants and animals had

become the subject of rapidly expanding research. Fifty years later, a century after the *Origin*, the molecular structure of a gene had been discovered. Now, some 60 years later, many complexities of molecular genetics have been investigated, although challenges remain.

The basis for heredity is an organism's genome, strands of DNA of enormous length duplicated in each of its cells. Segments of this DNA encode the amino acid sequences for several tens of thousands of different proteins, which compose much of each cell's structure and regulate its vital functions. Other segments encode a large variety of RNA molecules, which themselves (without translation into proteins) provide a diverse array of regulatory actions. An organism's DNA also includes parasitic components, which hitchhike on the mechanisms for duplication or which subvert the mechanisms for translation for its own purposes. All of these direct and indirect effects of DNA provide mechanisms for heredity and opportunities for variation.

The genome, we now know, is not the only way that parents can transmit their features to their progeny (Jablonka and Lamb 2014; Robert 2009). The cytoplasmic contents of ova (and sperm, in special cases) are transferred to zygotes and influence their development. The DNA in mitochondria is the primary example of maternal cytoplasmic inheritance, but other components of the cytoplasm can also influence development.

Bonding of methyl groups to nucleotide bases in a segment of DNA can decrease its rate of translation to proteins. This inactivation of DNA by methylation is catalyzed by enzymes encoded by DNA elsewhere in the genome. In some cases, methylation is also promoted by environmental conditions, such as temperature or stress. Furthermore, patterns of methylation are sometimes passed to progeny with the parents' DNA. Plants and animals differ in which nucleotide base is methylated (cysteine in animals, adenosine in plants) and also in the rates of transfer to progeny (greater in plants, which lack the isolated lines of germ cells in animals). Gradual loss of methylation in successive generations eventually attenuates its effects. Nevertheless, rates of methylation and rates of reversion vary markedly in different

regions of DNA (Van der Graaf et al. 2015). Yet whether or not patterns of methylation persist across many generations, natural selection can enhance or diminish their influence on the activity of DNA, just as it can adjust other molecular mechanisms that regulate expression of DNA. Methylation, often called “epigenesis,” meaning “beyond genetics,” expands the possibilities for natural selection. With its susceptibility to environmental influences and its progressive loss, it provides a mechanism for heredity more flexible and less stable than other ways to regulate DNA.

Still less stable influences on development, but nevertheless hereditary, can result from direct responses to an environmental feature sustained across generations. Learned habits and customs are examples that can propagate in families and populations of interacting individuals. The seasonal territorial boundaries defended by many songbirds, as well as features of their songs, provide examples of learned information transferred across generations in organisms other than humans.

Consider even a suggestion by Lamarck that persistent abrasion of parts of the body could result in inheritance of calloused skin. This “inheritance” would occur in human populations, for instance, if children tended to follow parents’ predominant activities, such as using hands for heavy work or bare feet for walking.

Direct environmental influences have often not been accepted as natural selection. Yet the capability for developing callouses, for instance, is likely to require a predisposition to respond to abrasion by thickening of the epidermis, and such a predisposition might depend on particular structural or regulatory proteins (or methylation of particular segments of DNA, or both), all of which would require particular variants of DNA. In other words, development of callouses would depend on a particular interaction of genes and environment. In this case, for a particular genetic structure of the organism, development of callouses would be especially sensitive to environmental conditions.

Other environmental influences on development, including learning, also require physiological mechanisms and predispositions to respond to

features of the environment and thus are also subject to adaptation by natural selection.

The result can take different forms. Development might vary continuously with some environmental feature. Alternatively, developmental switches might produce several alternatives in response to particular environmental features. In other cases, development might be especially sensitive to an individual’s genome, rather than to its environment. An example is human growth to a particular height, in a population of well-nourished individuals. In such cases, genetic influences are more or less “canalized” within a range of frequently encountered environments. Across the entire spectrum from predominant influences of the environment to predominant influences of the genome, the development of an organism is always an interaction of its particular genome and its particular environment.

The influences on an individual’s development span a spectrum of stability from genome to environment. DNA, one of the most stable organic molecules known, retains some of its structure even in the remnants of organisms that died tens of thousands of years ago. In contrast, the most variable features of the environment, for example the weather, can hardly be predicted from day to day. The development of an individual depends on responses to this entire spectrum of influences. At one end is an archival plan, at the other an immediate context.

No successful construction can rely on one of these alone, neither plan nor context. Context alone has too many possibilities; a plan has too few. Trying to build without a plan is just as likely to fail as insistence on following a plan. Successful construction, as much as successful development, results from adaptations at various levels of stability and flexibility. A “tried and true” plan is important. So is attention to immediate context. Success requires stability across generations as well as flexibility in momentary responses.

Development of an organism, its construction, is thus a plan instantiated in a particular context. All contextual influences during the lifetime of an organism, whether temperature, nutritional, or sensory, are mediated by proteins encoded by the genome. An individual’s response to any stimulus

depends on its current state as much as it does on the impinging stimulus. An individual's behavior, for instance, is at any instant an interaction between its present state and the incident stimulation. This interaction of current state and immediate environment continues through the successive, incremental stages of development, throughout an organism's life.

Each individual's survival and reproduction thus result from an interaction of its current state and its current environment. This process occurring in all individuals of a population produces natural selection. So the progressive interaction of genes and environment during an individual's development is embedded in a longer interaction of genes and environment in the evolution of a population of individuals. The pattern of an organism's development is embedded in the pattern of a population's evolution. Natural selection, an interaction between genomes and environment directing the evolution of a population, results from interactions of genome and environment directing the development of each organism.

As a result of such pervasive interaction, we can draw four general conclusions about structure and context: (1) nothing is *determined* by structure, (2) nothing is *determined* by context, (3) everything is *influenced* by structure, and (4) everything is *influenced* by context. In these four conclusions, the general terms, *structure* and *context*, summarize a variety of more specific alternatives: *plan* and *reality*, *physiological state* and *sensation*, *genotype* and *environment*. Each pair of alternatives, substituted for *structure* and *context* in the four statements, produces equally general conclusions.

Variation in Heritable Features

Natural selection, as just described, might produce stability or flexibility in development, to any degree between extremes of "canalization" and "plasticity." In any particular case, the result depends on the nature of both genetic variation and environmental variation.

Genetic variation in a population is produced by mutations in the genome, by genetic drift (random variation in reproduction or survival),

and by migration to and from other populations. R. A. Fisher (1930) first emphasized the importance of variation in his "Fundamental Theorem of Natural Selection," which states that evolution is proportional to genetic variation, for any strength of natural selection. G. R. Price generalized this equation, by partitioning the change in genotypes in a subsequent generation into the covariance between genes and environment. Price's equation makes it clear that this principle can apply to any change, including learning as well as evolution (Okasha 2008; Grafen 2015; Queller 2017). Variation is fundamental to natural selection just as it is to learning.

One consequence is that natural selection must depend on mutation rate. This rate determines the rate of increase in genetic variation in a population; the rate of decrease in genetic variation, in contrast, depends on random loss (genetic drift) and thus on the size of a population. Migration affects genetic variation also, but the principles are similar. Mutation rates, by their effects on natural selection, influence the rate at which a population adapts to environmental change.

The mutation rate at any locus in the genome depends on the regulation of duplication and repair of DNA by proteins encoded elsewhere in the genome. If so, mutation rates might evolve to adjust the stability of DNA at particular locations in the genome. Natural selection might adjust these rates to the rates at which relevant environmental features change. It is known that segments of DNA (and thus the corresponding proteins) differ in their mutation rates. Not well understood, however, is whether or not mutation rates themselves evolve to adjust the rate of evolution by natural selection at different places in the genome.

Environmental variation comes in a spectrum of periodicities, with durations from seconds to many centuries. The stability or plasticity of development or evolution depends on how natural selection responds to different degrees of environmental periodicity. Environmental variation with periods much shorter than an individual's life is best accommodated by direct influences of the environment on an individual's development. Environmental variation over periods of one or a few generations is often better accommodated by a few alternative sub-plans for development.

Variation over intervals of many generations is handled most efficiently by revisions of the basic plan. For biological organisms, these three alternatives correspond respectively to learning, developmental switches (Pfennig 1990), and genomic encoding. These three alternatives are of course points in a continuous spectrum from flexibility to stability. Each of these developmental alternatives results from an interaction of environment and genome, with progressively decreasing reliance on environmental flexibility and increasing reliance on genomic stability.

Nevertheless, the entire spectrum of developmental alternatives rests ultimately on the genome, the most stable form of inheritance. The genomes of organisms must encode the capabilities and predispositions for genetic or environmental stability, for developmental switches, for temporary methylation, or for flexible learning – for development in response to long-term, medium-term, or short-term variations in the environment. The development of individuals thus cannot be separated from the evolution of populations. Natural selection occurs at all periodicities of environmental variation.

Cooperation and Competition

The evolution of cooperation has created another challenge for natural selection. Darwin's initial summary of natural selection emphasized a "struggle for existence," inspired by Malthus' observation that reproduction can outrun resources for survival. This "struggle" implies competition. Ecologists now recognize two forms of competition, aggressive and exploitative. In the first case, direct interaction between two individuals results in greater access to a limiting resource for one of them. In the second, one individual acquires proportionately more of a resource as a result of its greater efficiency at locating or harvesting it, without any direct interaction with other individuals. Both forms of competition can result in the "struggle" Darwin imagined as the basis for natural selection. In his discussion of honeybees, Darwin acknowledged the challenge that such competition presents for the evolution of cooperation.

Simplistic explanations for the evolution of cooperation prevailed for more than a century after *The Origin of Species*. During the middle decades of the twentieth century, for instance, it was widely assumed that cooperation would prevail in a population whenever cooperating individuals gained an advantage over non-cooperators. Furthermore, it was assumed that competition between groups of cooperators and groups of non-cooperators would lead to the evolution of cooperation.

A path-breaking book, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, challenged these assumptions in their naive forms (Williams 1966, also Dawkins 1976). Cooperation might provide advantages to individuals and thus favor the spread of alleles associated with helping, but it is also necessary to consider possibilities for the spread of alleles associated with *exploitation* of cooperators. Such "cheaters" would have the benefit of accepting help from cooperators without the cost of reciprocating. Cooperators then face the prospect of becoming "suckers," by providing benefits to others that do not return them. Simple math shows that alleles associated with cheating spread at the expense of those associated with helping, even to elimination of the last helper alleles from a population. Group selection, the selection of cooperative groups in competition with non-cooperators, thus appeared in a new perspective. Cooperation had to spread *within* groups before it could spread by competition *between* groups.

Even if cooperation occurred mainly in small and relatively stable groups of individuals, so that some groups might by chance lack individuals with alleles for cheating and cooperators could prosper, these groups would remain vulnerable to any new alleles associated with cheating, which would then spread by natural selection to exclude cooperation.

Nevertheless, persistent cooperation has been documented for many kinds of organisms (Koenig and Dickinson 2016). It is clear, though, that special conditions apply. First, cooperation must spread within groups before it can spread by selection among groups. Second, reciprocity is a key to cooperation: costly helping must have compensating benefits in return. Third, alleles

associated with cooperation can propagate within families as a result of kin selection, a special case of natural selection.

The evolution of cooperation under these constraints requires alleles associated with a behavioral tactic more complex than a simple heritable tendency to help. Perhaps the simplest effective tactic is to try helping occasionally but to continue only if reciprocation ensues (“win stay, lose shift” or WSLS). For instance, sedentary individuals, restricted to interacting repeatedly with a few neighbors, can evolve neighborhoods of cooperation, provided neighbors have alleles predisposing them to initial cooperation rather than cheating. More effective is a capability for identifying and tracking individual partners (Wiley 2012, 2015). Alleles associated with tit for tat (WSLS directed at recognizable partners) then permit a cooperative resolution of the prisoner’s dilemma. With further behavioral elaboration, individuals might have capabilities for tracking multiple partners. Then alleles associated with such tracking (combined with those for predictable reputations of helping others) can make diffuse reciprocity advantageous (Nowak 2006; Nowak and Highfield 2011).

A different sort of advantage accrues to helping when it is directed toward genealogical relatives. In kin selection, an allele associated with helping kin can spread provided the cost to the helping individual is less than the benefit to its relative, devalued by the probability that the relative carries a copy of the same allele (in excess of the probability in the population at random). The mathematical condition is $C < rB$, where r is the coefficient of genealogical relatedness (the relevant probability when an allele for helping is rare). Individuals do not have to recognize kin directly; they can reliably interact with kin simply as a result of, for instance, birth in the same nest.

Investigation of a wide variety of animals and human societies shows that helping is frequently directed to close kin. Nevertheless, clear exceptions occur. Furthermore, it is rare that the quantitative condition, $C < rB$, is met. The latter difficulty can be overcome by a combination of some reciprocity in addition to close kinship. Kinship and reciprocity should complement each

other in the evolution of cooperation by natural selection.

A further complexity can favor the evolution of cooperation within groups: policing. If cooperators join forces to punish or exclude cheaters, the extra cost imposed on cheating can make it less competitive in relation to cooperation. In this case, the cost to cooperators of policing must not reduce the benefits of cooperation too much. Also, avoiding the costs of policing (while yet enjoying its diffuse benefits) becomes a second-order form of cheating. Finally, if policing results in the expulsion of cheaters from a group, so cheaters face the possibility of receiving no benefit whatsoever from membership in the group, then selection might favor a form of stealth-cheating by sophistication in evading detection. Alternatively, super-cheating might consist of complete disruption of a group in the expectation that strictly individual competition might provide greater advantages for a cheater than expulsion from a cooperative group.

This spectrum of possibilities for the evolution of cooperation by natural selection involves increasing behavioral complexity. Some of the options thus might apply only to humans. For instance, although cooperative interactions with kin are widespread among nonhuman animals, only a few nonhuman primates have enough complexity of individual recognition to support the formation of reputations (Wiley 2012). Evidence for policing by animals, even primates, is also sparse (Flack et al. 2005; Beisner and McCowan 2013). On the other hand, neither theory nor field work has yet plumbed the complexities of helping and cheating, either animal or human.

Constraints on Natural Selection

In the early years of population genetics, a controversy arose between two of the pioneers in this field. Fisher’s Fundamental Theorem suggested that natural selection would move populations in a particular environment toward ever greater adaptation provided a source of genetic variation, such as mutation, persisted. Sewall Wright argued, on the other hand, that natural selection usually moved populations toward a local

optimum in an adaptive landscape with multiple optima. An adaptive landscape, as Wright imagined it, is a multidimensional map of the adaptation of organisms as a function of possible genotypes, in other words, of all possible combinations of alleles at every genetic locus (Wright 1932, 1986). An adaptive landscape in this sense applies to a particular environment. Only if each allele evolved independently would natural selection lead to a unique, maximally adapted genotype for this environment, as Fisher indicated.

Interactions among alleles, as Wright argued, make multiple local optima for genotypes nearly inevitable. Constraints on interactions of alleles at the same locus or at different ones would produce adaptive peaks in any environment. Optima in such an adaptive landscape result from trade-offs in the interactions of alleles at the same or different loci, in one or multiple individuals. Such interactions are frequent in genomes and populations. Any one protein often affects more than one cellular function or trait (pleiotropy), and any one trait or function is often influenced by more than one protein (epistasis). A change in one trait might benefit survival or reproduction only if a concurrent change occurs in another trait. Furthermore, social interactions can involve traits with advantages for one individual but disadvantages for another, or traits with advantages only when present in both individuals concurrently.

Alleles associated with such traits often do not spread in a population when rare. For instance, during sexual selection, alleles associated with a female preference for a male trait do not spread unless their frequency in the population exceeds a threshold (or their genetic correlation with alleles for the male trait exceeds a threshold) (Lande 1981; Kirkpatrick 1982; Andersson 1994). In general, alleles associated with producing a signal cannot spread when alleles for responding to the signal are too infrequent, even if a response would benefit a signaler. Vice versa, alleles for responding cannot spread when alleles for signaling are rare, even if a response to a signal would benefit the receiver. Only in a population with enough of both sorts of alleles can they both spread (Wiley 2015).

The situation is even more constrained when rare traits have costs for individuals. For instance, when a preference takes time or a signal entails exposure to predators, these individuals are often subject to increased mortality when their counterparts are not quickly located. The associated alleles are lost from the population by natural selection even more rapidly than by random genetic drift alone. Furthermore, alleles for mate preferences interact in counter-intuitive ways with those for ecological differences (Servedio and Kopp 2012; Servedio and Bürger 2014).

Interactions between heritable variants, whether pleiotropic or epistatic, place constraints on evolution by natural selection. Thresholds and isolated adapted optima result. Only genetic drift or extraordinary mutations can move populations past hurdles or valleys where genotypes are associated with disadvantageous traits of organisms (phenotypes). Because alleles cannot persist unless organisms associated with them survive and reproduce disproportionately, thresholds and isolated optima are not easily surpassed. When multiple traits or genes are required for an overall advantage in survival and reproduction, the probability of overcoming disadvantages decreases.

In some cases, it is possible to circumvent hurdles by coopting unrelated traits or functions (Wiley 2017). In the course of natural selection, fins can become repurposed as legs and wings, just as ocelli can become photographic eyes, comfort movements can become signals, and perhaps habituation can become associative learning. Without cooptation of simpler traits to produce more complex ones, natural selection can overcome thresholds and isolated optima only by waiting for fortuitous mutations, either simultaneous combinations or discontinuous effects, occurrences sometimes called “hopeful monsters.” Perhaps, in the long run, such events can occur. If so, evolution would inevitably lead to maximal adaptation of organisms, as Fisher indicated, despite the thresholds and local optima created by interacting alleles in the short run. Nevertheless, these interactions prolong, even when they do not prevent, evolution toward global optima by natural selection.

Empirical studies of natural selection have so far infrequently reported pleiotropy and epistasis of alleles under selection (Kingsolver and Diamond 2011). Perhaps these interactions in fact seldom constrain natural selection. On the other hand, the constraints might make selection more difficult to study, so that reports have focused on selection with little constraint. It is also possible that selection itself, over sufficient time, tends to reduce these constraints. For instance, duplication of a gene occurs frequently in the course of evolution, often followed by differentiation of the functions of the “daughters.” Duplication and subsequent differentiation would reduce the constraints of pleiotropy on further progress of natural selection. The mechanism of duplication is itself regulated by other proteins and thus subject to evolution by natural selection.

Interactions between alleles at the same or different locations in DNA or between different consequences of the same allele, and the corresponding interactions between traits of organisms, all produce constraints on the progress of evolution by natural selection. As the complexity of organisms increases, it seems possible that these constraints become ever more complex and thus the constraints on evolution by natural selection ever more obstructive. Natural selection itself might produce still more complex genomes to reduce these constraints somewhat.

Evolutionary Computation

Biological evolution is not the only framework for discussing natural selection. Nothing precludes a generalization of its principles far beyond biological evolution. Optimizing structure by means of heritable variation and selection applies equally to evolution, epigenetics, and learning. In recent decades, it has also been applied to computation and molecular synthesis.

Evolutionary computing provides a way to optimize an algorithm (analogous to optimizing genetic structure) by systematically modifying its components (mutation) and then selecting those versions of components that optimize the output (organism or phenotype) for particular purposes

(environments). The process is usually incremental and progressive like natural selection in biological evolution: mutation and selection occur repeatedly until a local optimum is reached.

An example is the use of neural networks to discriminate sets of inputs. In this case, a series of similar inputs is presented to a network of interacting nodes, each of which can promote or inhibit activity in other nodes and all of which combine to provide a response to each input. Randomly adjusting the interactions of nodes at each generation and then selecting those variants that improve discrimination between different sets of inputs eventually yields the best performance possible. In a similar way, pharmacologists search for optimal molecular structures by progressively altering the components of complex molecules (for instance, the sequences of amino acids in synthesized proteins) in order to maximize medical benefits and to minimize undesirable side-effects.

Evolutionary computing or adaptive synthesis occurs in a multidimensional adaptive landscape just as biological evolution does. The adaptive landscape is the performance of an algorithm or synthetic molecule as a function of the hyperspace of possible structures (nodes and parameters or types and positions of chemical functional groups). Any solution encounters two widely discussed problems: too much precision to capture an entire adaptive peak; and too little accuracy to capture a global peak. In evolutionary computing, the first problem is called “overfitting” (Domingos 2012; Srivastava et al. 2014); it applies to algorithms that perform well on initial data but poorly on similar, but previously unseen, data. Such an algorithm has evolved to a local peak but too narrowly. In other words, an algorithm with overfitting has learned some of the noise (non-generalizable features) in the initial data as well as some of the signal (generalizable features). It has learned too much.

Ways to reduce overfitting include early stopping (as soon as errors on previously unseen data increase too steeply) and limitations on structural and parametric complexity (by reducing the number of nodes and interactions and their weights). Constraining weights of parameters often reduces

overfitting by reducing the unpredictability of responses to similar but previously unseen data. All of these procedures rely on testing algorithms with unseen data. In terms of an adaptive landscape, they require testing performance on nearby parts of the landscape.

The second problem of evolutionary computing also has its analogue in biological evolution. Natural selection moves structures toward adaptation to a local optimum in the adaptive landscape and thus can miss a global optimum. Any algorithm, just as any population of organisms, evolves adaptation only to those inputs, variable or not, that it encounters. The only way to be sure of finding a global optimum is to test performance throughout the multidimensional adaptive landscape of possible structures. To assure finding this maximum, in the most general case, would require understanding the complete multidimensional structure and connections of the entire universe, down to the last quark. No advance in evolutionary computing, even as quantum computers increase the speed and breadth of learning or adapting, can guarantee discovery of a global maximum (Niu et al. 2019).

These problems in evolutionary computing have parallels in biological evolution. The generality and specialization of algorithms, we noted, can be probed by varying the environment. For natural populations, such probing of adaptations occurs when an environment varies in time. To acknowledge this variation, it has been suggested that a better metaphor is evolution in an “adaptive seascape.” Adaptations of organisms are thus like well-fitted algorithms, both of which perform well over a local optimum with a spectrum of periodicities in input. Yet they do not necessarily perform well in similar environments not previously experienced. Organisms, including human engineers, instead settle for adaptation to a (not too) local optimum.

Humans making decisions with the assistance of evolutionary computing have learned to extend the principles of natural selection. Making decisions based on trial and error, whether by brains alone or by brains assisted by machines, results in optimal responses to each of numerous inputs. It is the basic process of human behavior. Indeed all

animals, not just humans, learn to match responses to inputs. Decisions occur whenever an organism discriminates between alternative inputs when choosing what to eat or where to go or whom to associate with or to imitate. They do so because decisions in response to unpredictable inputs allow greater specificity in adaptations. An organism’s capabilities and predispositions are specified by a stable plan, the organism’s genome. Such a plan, as discussed above, is the basis for all forms of learning and culture. This plan then develops in conjunction with its immediate context, the organism’s environment. Evolutionary computing is thus itself a result of evolution by natural selection.

Conclusion

Every organism develops from a particular plan in a particular environment. It persists as long as repair of its molecular components can counteract degradation – as long as its immediate structure can harvest exogenous energy to counteract entropy. Each organism, each instantiation of its plan, eventually decays. Yet, provided an organism transmits its original plan to nascent progeny, a similar organism in a similar environment can develop anew. Provided organisms transmit their plans to progeny with some appropriate level of variability, natural selection can yield a lineage of organisms that persists indefinitely in an environment of complex changes. Organisms with adaptations for learning can improve their survival in environments with short-term variation. These adaptations can extend even to learning the principles of natural selection. In the end, entropy, the ultimate noise in decisions, prevents learning with infallible foresight – and prevents immortality.

In a population of comparable entities, natural selection is no more than the spread of heritable variants that replicate at a higher rate than others. Natural selection is arithmetic applied to differences. The principles are the same in all cases. The mechanisms of heredity vary across a spectrum of stability, from the relative inflexibility of the genome to the increasing flexibility of developmental switches, epigenesis, and learning, even to

quantum computing. Each mechanism is optimized for a pertinent environment by selection itself. Natural selection is potentially constrained by interactions within and between the entities in a population. It leads to greater complexity whenever it can produce more precise and accurate adaptations. The scope of evolution by natural selection thus includes the evolution of culture, cognition, and language. It thus leads to brains so large that they strain the limits of skeletal adaptations. The scope enlarges still further to include even those decisions assisted by machines.

Finally, consider several misconceptions about natural selection. Each misconstrues issues addressed above. All contradict evidence or logic.

The first misconception claims that culture is distinct from biology and thus not subject to natural selection. On the contrary, environment and genome interact in the development of all organisms, including humans. All features of an organism, including their predispositions and capabilities for learning, are influenced by their genetic structure, just as all features of an organism are also influenced by their environmental context.

Another misconception is that natural selection cannot accommodate Lamarckian evolution, in other words inheritance of environmental influences on individuals. We now know that such environmental influences can affect progeny, but natural selection produces and regulates the necessary mechanisms for these influences.

A third misconception is that natural selection, inasmuch as it is a selection, implies the existence of a selecting agent. Darwin was aware of this difficulty with the term “selection.” Clearly rejecting any such agent, he nevertheless felt there was no succinct alternative for the term. Despite any limitations of language, there is no agent of selection.

Finally, it is sometimes claimed that selected individuals are morally superior. On the contrary, natural selection results from the arithmetic of survival and reproduction of genetic variants in limited populations. It has no more moral implications than any other example of arithmetic. Morality (ethics) instead applies to human attitudes toward the various consequences

of natural selection. Because such behavioral dispositions are influenced by genes and by context, they are themselves influenced by natural selection.

Natural selection is not the child of morality; instead, morality is the child of natural selection. And not only morality but also philosophy. In the end, natural selection produces not only a philosophy of biology, but also a biology of philosophy.

Cross-References

- ▶ [Evolution of Communication](#)
- ▶ [Evolution of Cooperation](#)
- ▶ [Evolution of Free Will](#)
- ▶ [Evolution of Self-consciousness](#)
- ▶ [Frequency-Dependent Selection](#)
- ▶ [Genetic Predispositions](#)
- ▶ [Genetic Relatedness](#)
- ▶ [Group Selection](#)
- ▶ [History of Natural Selection](#)
- ▶ [Kin Selection](#)
- ▶ [Sexual Selection](#)
- ▶ [Tit-for-Tat Cooperation](#)

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