A2.1 Principles of evolutionary processes

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Abstract

The principles of evolution are considered. Evolution is seen to be the inevitable outcome of the interaction of four essential processes: reproduction, competition, mutation, and selection. Consideration is given to the duality of natural organisms in terms of their genotypes and phenotypes, as well as to characterizing evolution in terms of adaptive landscapes.

A2.1.1 Overview

The most widely accepted collection of evolutionary theories is the neo-Darwinian paradigm. These arguments assert that the vast majority of the history of life can be fully accounted for by physical processes operating on and within populations and species (Hoffman 1989, p 39). These processes are reproduction, mutation, competition, and selection. Reproduction is an obvious property of extant species. Further, species have such great reproductive potential that their population size would increase at an exponential rate if all individuals of the species were to reproduce successfully (Malthus 1826, Mayr 1982, p. 479). Reproduction is accomplished through the transfer of an individual's genetic program (either asexually or sexually) to progeny. Mutation, in a positively entropic system, is guaranteed, in that replication errors during information transfer will necessarily occur. Competition is a consequence of expanding populations in a finite resource space. Selection is the inevitable result of competitive replication as species fill the available space. Evolution becomes the inescapable result of interacting basic physical statistical processes (Huxley 1963, Wooldridge 1968, Atmar 1979).

Individuals and species can be viewed as a duality of their genetic program, the *genotype*, and their expressed behavioral traits, the *phenotype*. The genotype provides a mechanism for the storage of experiential evidence, of historically acquired information. Unfortunately, the results of genetic variations are generally unpredictable due to the universal effects of pleiotropy and polygeny (figure A2.1.1) (Mayr 1959, 1963, 1982, 1988, Wright 1931, 1960, Simpson 1949, p 224, Dobzhansky 1970, Stanley 1975, Dawkins 1986). Pleiotropy is the effect that a single gene may simultaneously affect several phenotypic traits. Polygeny is the effect that a single phenotypic characteristic may be determined by the simultaneous interaction of many genes. There are no one-gene, one-trait relationships in naturally evolved systems. The phenotype varies as a complex, nonlinear function of the interaction between underlying genetic structures and current environmental conditions. Very different genetic structures may code for equivalent behaviors, just as diverse computer programs can generate similar functions. A2.2.2

Selection directly acts only on the expressed behaviors of individuals and species (Mayr 1988, pp 477–8). Wright (1932) offered the concept of adaptive topography to describe the fitness of individuals and species (minimally, isolated reproductive populations termed demes). A population of genotypes maps to respective phenotypes (*sensu* Lewontin 1974), which are in turn mapped onto the adaptive topography (figure A2.1.2). Each peak corresponds to an optimized collection of phenotypes, and thus to one of more sets of optimized genotypes. Evolution probabilistically proceeds up the slopes of the topography toward peaks as selection culls inappropriate phenotypic variants.

Others (Atmar 1979, Raven and Johnson 1986, pp 400–1) have suggested that it is more appropriate to view the adaptive landscape from an inverted position. The peaks become troughs, 'minimized prediction

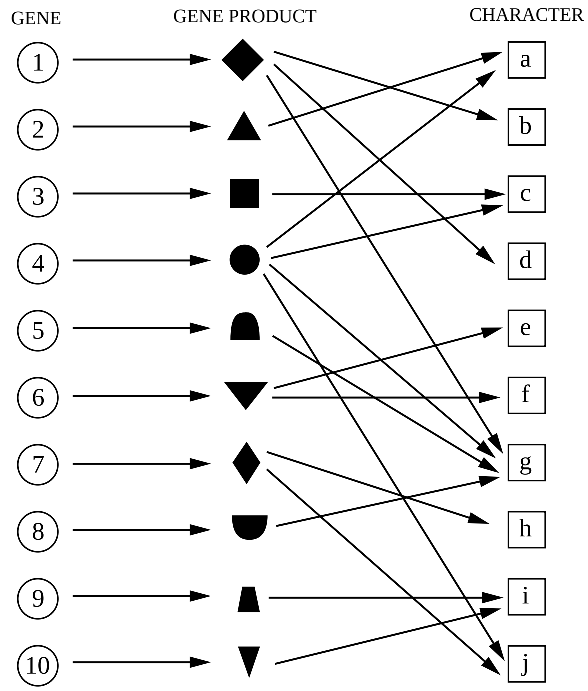

Figure A2.1.1. Pleiotropy is the effect that a single gene may simultaneously affect several phenotypic traits. Polygeny is the effect that a single phenotypic characteristic may be determined by the simultaneous interaction of many genes. These one-to-many and many-to-one mappings are pervasive in natural systems. As a result, even small changes to a single gene may induce a raft of behavioral changes in the individual (after Mayr 1963).

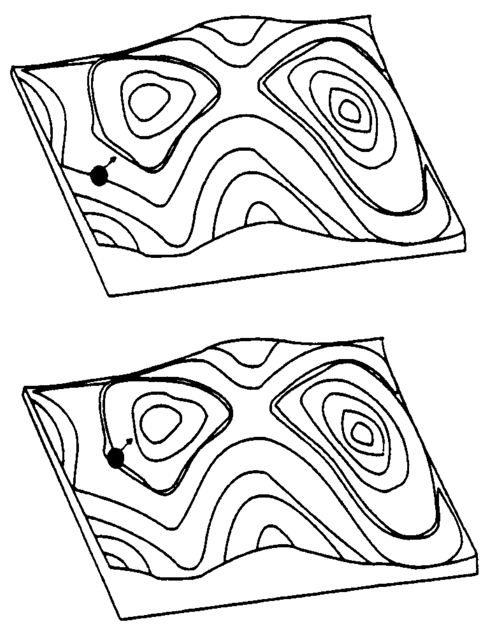

Figure A2.1.2. Wright's adaptive topography, inverted. An adaptive topography, or adaptive landscape, is defined to represent the fitness of all possible phenotypes (generated by the interaction between the genotypes and the environment). Wright (1932) proposed that as selection culls the last appropriate existing behaviors relative to others in the population, the population advances to areas of higher fitness on the landscape. Atmar (1979) and others have suggested viewing the topography from an inverted perspective. Populations advance to areas of lower behavioral error.

error entropy wells' (Atmar 1979). Searching for peaks depicts evolution as a slowly advancing, tedious, uncertain process. Moreover, there appears to be a certain fragility to an evolving phyletic line; an optimized population might be expected to quickly fall of the peak under slight perturbations. The inverted topography leaves an altogether different impression. Populations advance rapidly down the walls of the error troughs until their cohesive set of interrelated behaviors is optimized, at which point stagnation occurs. If the topography is generally static, rapid descents will be followed by long periods of stasis. If, however, the topography is in continual flux, stagnation may never set in.

Viewed in this manner, evolution is an obvious optimizing problem-solving process (not to be confused with a process that leads to perfection). Selection drives phenotypes as close to the optimum as possible, given initial conditions and environment constraints. However the environment is continually changing. Species lag behind, constantly evolving toward a new optimum. No organism should be viewed as being perfectly adapted to its environment. The suboptimality of behavior is to be expected in any dynamic environment that mandates tradeoffs between behavioral requirements. However selection never ceases to operate, regardless of the population's position on the topography.

Mayr (1988, p 532) has summarized some of the more salient characteristics of the neo-Darwinian paradigm. These include:

(i) The individual is the primary target of selection.
(ii) Genetic variation is largely a chance phenomenon. Stochastic processes play a significant role in evolution.
(iii) Genotypic variation is largely a product of recombination and 'only ultimately of mutation'.
(iv) 'Gradual' evolution may incorporate phenotypic discontinuities.
(v) Not all phenotypic changes are necessarily consequences of *ad hoc* natural selection.
(vi) Evolution is a change in adaptation and diversity, not merely a change in gene frequencies.
(vii) Selection is probabilistic, not deterministic.

These characteristics form a framework for evolutionary computation.

References

Atmar W 1979 The inevitability of evolutionary invention, unpublished manuscript
Dawkins R 1986 *The Blind Watchmaker* (Oxford: Clarendon)
Dobzhansky T 1970 *Genetics of the Evolutionary Processes* (New York: Columbia University Press)
Hoffman A 1989 *Arguments on Evolution: a Paleontologist's Perspective* (New York: Oxford University Press)
Huxley J 1963 The evolutionary process *Evolution as a Process* ed J Huxley, A C Hardy and E B Ford (New York: Collier) pp 9–33
Lewontin R C 1974 *The Genetic Basis of Evolutionary Change* (New York: Columbia University Press)
Malthus T R 1826 *An Essay on the Principle of Population, as it Affects the Future Improvement of Society* 6th edn (London: Murray)
Mayr E 1959 Where are we? *Cold Spring Harbor Symp. Quant. Biol.* **24** 409–40
——1963 *Animal Species and Evolution* (Cambridge, MA: Belknap)
——1982 *The Growth of Biological Thought: Diversity, Evolution and Inheritance* (Cambridge, MA: Belknap)
——1988 *Toward a New Philosophy of Biology: Observations of an Evolutionist* (Cambridge, MA: Belknap)
Raven P H and Johnson G B 1986 *Biology* (St Louis, MO: Times Mirror)
Simpson G G 1949 *The Meaning of Evolution: a Study of the History of Life and its Significance for Man* (New Haven, CT: Yale University Press)
Stanley S M 1975 A theory of evolution above the species level *Proc. Natl Acad. Sci. USA* **72** 646–50
Wooldridge D E 1968 *The Mechanical Man: the Physical Basis of Intelligent Life* (New York: McGraw-Hill)
Wright S 1931 Evolution in Mendelian populations *Genetics* **16** 97–159
——1932 The roles of mutation, inbreeding, crossbreeding, and selection in evolution *Proc. 6th Int. Congr. on Genetics (Ithaca, NY)* vol 1, pp 356–66
——1960 The evolution of life, panel discussion *Evolution After Darwin: Issues in Evolution* vol 3, ed S Tax and C Callender (Chicago, IL: University of Chicago Press)