# NATURAL SELECTION AND THE EFFECTS OF ECOLOGICAL INTERACTION ON POPULATIONS

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**Summary**

Understanding the processes of evolution rests on two areas of biological investigation: population genetics and population ecology. The notion that ecology plays a central role in the dynamics of population biology and, ultimately, in the formation of new species, is at least as old as the modern evolutionary synthesis. Historically, however, more attention has been focused on the study of speciation by purely genetic mechanisms.

But, it is only within an ecological perspective that the events leading from genetic dynamics within populations to global biodiversity can be approached and possibly

understood.

The concept of environment has been sometimes applied to individuals, populations, and communities. The current notion is that only individuals have an environment and hence represent the units of natural selection, but it is only at the level of population that microevolutionary processes occur. In this perspective, the population is the unit of evolution, because this is the spatial and temporal level where genotypes, with their phenotypic flexibility, experience ecological interactions and are forwarded to the next generations.

Depending on the aspect or level of population biology on which attention is focused, different kinds of natural selection can be addressed. Different selective models do not necessarily exclude each other: under given ecological conditions, a given population may experience more than one form of selection. Classifying natural selection under several categories is often subjective; it reflects our difficulty to understand complex, dynamic processes and the need to divide them into simpler, more approachable issues.

An understanding of spatial population dynamics is crucial when attempting to depict microevolutionary trends. The metapopulation concept may help us to better describe how natural populations and species answer the challenge of ecological constrains, and how natural selection acts in modeling their genetic structure.

The ultimate outcome of all genetic dynamics and environmental interactions is speciation, the process that gives rise to new separate, non-interbreeding units. Although the process of speciation is not classically regarded as a direct result of natural selection, recent evidence accounts for a role of disruptive and sexual selection in determining reproductive barriers.

Ecological processes are a central issue, because they are the agents of natural selection, but exactly how, and to what degree, they contribute to the formation of new species remains an open question in evolutionary biology.



## 1. Introduction

While examining the processes of evolution driven by natural selection, two areas of biological investigation must be considered: population genetics, which describes the dynamics of genetic variants that have arisen by mutation or recombination within a group of interbreeding organisms, and population ecology, which describes the interactions between these variants and the organisms' environment.

A species may be envisioned as an isolated pool of genes flowing through space and time, constantly adapting to changes in its environment and to the new environments encountered when extending its geographic range. At various intervals of time and in different environments, portions of this gene pool may become isolated and encounter new ecological conditions. Such isolated populations may become extinct, reunite with the parental population or may occasionally differentiate during isolation to form new species.

Originally, the concept of environment was applied equally to individuals, populations, and communities and sometimes even to ecosystems. The current notion is that only an individual has an environment. This means that all other members of an individual's own species are considered part of its environment. Environmental factors may be classified under four general components. This classification has proven extremely useful for organizing ecological studies, and for defining field and experimental protocols. These components are:

1. abiotic factors: physical aspects of the environment, such as climate (precipitation, wind, humidity, temperature) or altitude, day length, water depth, water chemistry, tides, etc.
2. food: usually other organisms, but includes nutrients for plants, and inorganic compounds for chemotrophic microorganisms
3. other organisms:
   (a) different species: competitors, predators, pathogens, symbionts etc.
   (b) same species: mates, family members, social groups etc.
4. place in which to live: other requirements, such as nest sites, shelter etc.

Ecology and genetics together form the mechanisms of evolutionary change. Genetic variability within populations for phenotypic characters that are ecologically important determines the speed and direction of the populations' response to selection resulting from ecological interactions. The ecological interactions of organisms with the biotic and abiotic environment are the context of natural selection. The ecological structure of populations also determines the potential for genetic drift, which is non-adaptive genetic change in populations. To understand the potential for, and constraints on, evolution in populations, one must consider both ecological and genetic issues. Further context is provided by placing the analysis of contemporary populations into a phylogenetic context, either through phylogeographic analyses within species or through broader systematic analysis of sets of taxa. Ecological genetics is thus a point of view in which awareness of variability among organisms is involved in the study of all kinds of ecological interactions, both biotic and abiotic. In this outlook, key ecological parameters are not considered fixed properties of populations or species, but are acknowledged to evolve in an ongoing feedback between ecology and genetics.



## 1.1 Adaptation and Evolution

In order to understand evolution, it is necessary to view populations as a collection of individuals, each harboring a different set of traits. A single organism is never typical of an entire population unless there is no variation within that population. Individual organisms do not evolve, they retain the same genes throughout their life. New traits arise in a population by changes or mutations that occur occasionally in the individual genome. Mutations are random and can arise by a variety of means, including those that are induced by some external agent (e.g., radiation, chemicals, viruses, etc.) or spontaneously as a result of replication errors that occur in the DNA. These changes may cause a significant change in a gene, which may result in a corresponding alteration in the phenotype of an individual. The environment provides the background upon which alternate forms of the same gene or traits are tested and whether these are beneficial, neutral, or detrimental to the survivability of certain individuals in a population. Under different environments, certain individuals have an "adaptive" edge or higher likelihood of surviving than other individuals, and consequently have greater potential to leave more offspring than less fit individuals. This non-random process is referred to as natural selection. According to Charles Darwin and Alfred Wallace, these changes accumulate over time in a population and provide the source of the adaptations observed in a species. Over long periods of time, this process can deepen divergence in populations to the point that new species arise. Thus, the process of evolution can be summarized in three steps: genes mutate, individuals are selected and populations evolve.

Evolution is not progress. Populations simply adapt to their current surroundings. They do not necessarily become better in any absolute sense over time. A trait or strategy that is successful at one time may be unsuccessful at another. Moreover, organisms are not passive targets of their environment, and species do not simply change to fit their environment, but they modify their environment to suit them as well. Alternately, when the environment changes, species can migrate to suitable microenvironments or seek out ones to which they are adapted.

## 2. Natural Selection

Adaptation and evolutionary change occur by the accumulation and summation of genotypic changes. Mutations are the source of new genetic variation on which natural selection operates. Natural selection is the only mechanism of adaptive evolution and it is defined as differential reproductive success of pre-existing classes of genetic variants in the gene pool. Those individuals favored by the environment will contribute more offspring to the next generation and will thus increasingly replace the less fit ones. In this sense, natural selection results in the passage of some genotypes into succeeding generations to a greater extent than for other genotypes. Enhancement of survival value can be achieved by one and/or the other of the following adaptive responses:

1. increased rate of reproduction (i.e., preference in mating, larger number of eggs laid, parental care, etc.);
2. decreased vulnerability to the environmental agents responsible for mortality (i.e., greater success in finding food supply, defence from predators, resistance to parasites etc…).

The most common action of natural selection is to remove unfit variants as they arise via mutation. In other words, natural selection usually prevents new alleles from increasing in frequency.

Natural selection may not lead a population to have the optimal set of traits. In any population, there would be a certain combination of possible alleles that would produce the optimal set of traits (the global optimum); but there are other sets of alleles that would yield a population almost as adapted (local optima). Transition from a local optimum to the global optimum may be hindered or forbidden because the population would have to pass through less adaptive states to make the transition. Natural selection only works to bring populations to the nearest optimal point. This idea is Sewall Wright's adaptive landscape, and represents one of the most influential models that shape the current view of evolution.

Natural selection does not have any foresight. It only allows organisms to adapt to their current environment. Structures or behaviors do not evolve for future utility, but rather existing ones are adopted and modified in an opportunistic way. As the environment changes, new traits may be selected for. Large changes in populations are the result of cumulative natural selection. Changes are introduced into the population by mutation; the small minority of these changes that result in a greater reproductive output of their bearers are amplified in frequency by selection.

The common phrase "survival of the fittest" is often used synonymously with natural selection. The phrase is both incomplete and misleading. Survival is only one component of selection and perhaps one of the less important ones in many populations. For example, in polygynous species, a number of males survive to reproductive age, but only a few ever mate. Males may differ little in their ability to survive, but vary greatly in their ability to attract mates. The difference in reproductive success stems mainly from the latter consideration. Also, the word ‘fit’ is often confused with physically fit. The evolutionary definition of fitness is the average reproductive output of a class of genetic variants in a gene pool. Fitter does not necessarily mean bigger, faster or stronger.

Many cases of natural selection seem obvious: camouflage to escape detection by a predator, thorns from stipules, epidermal outgrowths, stems, or leaves to prevent herbivory, substrate specialization by a fungus, and others. Nevertheless, empirical studies that demonstrate the existence of natural selection are scarce, because detection and monitoring of natural selection in real populations is inherently difficult.



### 2.1. The Different Aspects of Natural Selection

Natural selection can be studied by examining its effects on the observable characteristics, or phenotypes, of individuals in a population and the population as a whole. Depending on which different aspects or levels of population biology attention is focused, selection can be classified in several types: stabilizing, directional or disruptive; sexual selection; density-dependent or frequency-dependent; individual, kin, group or species selection; direct or indirect.

This cataloguing reflects the necessity to classify under fixed categories events that by definition are dynamic. Models do not necessarily exclude each other, in that under given ecological conditions, a population may experience more than one form of selection. Moreover, not all combinations of the different types of selection are equally likely or logically possible.

#### 2.1.1. Stabilizing Selection

Phenotypic traits, such as height, weight, number of offspring, and life span, typically show greater numbers of individuals with average characteristics and fewer towards the extremes. A situation such as this, where individuals with intermediate phenotypes are favored and extreme phenotypes are selected against, is referred to as stabilizing selection, or also as normalizing or optimizing selection.

Stabilizing selection is very common because the individuals that survive and reproduce more successfully are those that have intermediate phenotypic values. Mortality among newborn infants, for example, is highest when they are either very small or very large. Infants of average size are generally more likely to survive. As a result of stabilizing selection, populations often maintain a steady genetic constitution with respect to many traits. This attribute of populations is called genetic homeostasis.

Stabilizing selection can maintain or deplete genetic variation, depending on how it acts. When conditions are unchanging, stabilizing selection tends to reduce the amount of variation in the phenotype distribution. Genetic variance can be reduced by creating negative correlations of allelic effects (linkage disequilibrium) or by changing gene frequencies to be closer to fixation. The range and distribution of phenotypes then remains approximately the same from one generation to another.

Stabilizing selection has been demonstrated for ecologically important characters. A typical case is selection on clutch size in birds. The clutch size is the number of eggs laid, and is usually heritable. Birds feeding their nestlings are under two conflicting pressures: the more eggs are laid, the more potential surviving offspring are produced. However, as more eggs are laid, the more mouths there are to be fed after hatching. There is a limit on the amount of food the parents can bring back, and this means that for larger broods, the amount of food per offspring will start to decline. This could reduce the parent's success at contributing recruits to the breeding population. The phenomenon has been studied experimentally in a number of bird species. One of the best examples is that of the Collared Flycatcher, *Fidecula albicollis*, studied on an island in the Baltic Sea. An important feature of stabilizing selection is that the favored mean value may vary from place to place. So there can be local variation in the pattern of stabilizing selection. There is evidence that this is true for clutch size in birds. This has been shown in Europe for the blue tit and the great tit. The observation is that smaller clutch sizes are favored in poor habitats, such as suburban gardens, than in good habitats, such as mature deciduous woodland. There can also be temporal variation in stabilizing selection; in other words, different clutch sizes can be favored at different times within the same population.

When heterozygotes are more fit than either of the homozygotes, however, selection causes genetic variation to be maintained. This is called **balancing selection** or selection favoring heterozygotes. The classic example of this is the maintenance of sickle-cell alleles in human populations subject to malaria. Variation at a single locus determines whether red blood cells are shaped normally or sickle-shaped. If a human has two alleles for sickle-cell, he/she develops anemia because the shape of sickle-cells does not allow them to carry normal levels of oxygen. However, heterozygotes who have one copy of the sickle-cell allele, coupled with one normal allele enjoy some resistance to malaria. Indeed, the shape of sickled cells make it harder for the plasmodia (malaria causing agents) to enter the cell. Thus, individuals homozygous for the normal allele suffer more malaria than heterozygotes. Individuals homozygous for the sickle-cell are anemic. Heterozygotes have the highest fitness of these three types. Heterozygotes pass on both sickle-cell and normal alleles to the next generation. Thus, neither allele can be eliminated from the gene pool. The sickle-cell allele is at its highest frequency in regions of Africa where malaria is most pervasive.

Balancing selection is rare in natural populations. Only a handful of other cases beside the sickle-cell example have been found. At one time, population geneticists thought balancing selection could be a general explanation for the levels of genetic variation found in natural populations. That is no longer the case. It has also been demonstrated on theoretical grounds that natural selection cannot maintain polymorphisms at several loci via balancing selection.

### 2.1.2. Directional Selection

Directional selection favors traits that are at one extreme of a range of traits in a population. Traits at the opposite extreme or in the center of the distribution are selected against. If directional selection continues for many generations, the favored traits become more and more extreme, leading to distinct changes in the allele frequencies of the population. Directional selection occurs because of continued and directional changes in the climate, topographic and geographic features, or in other organisms, whether predators, prey, parasites, or competitors. The opportunity for directional selection also arises when organisms colonize new environments where the conditions are different from those of their original habitat. In addition, the appearance of a new favorable allele, as a result of gene flow or mutations, or a new genetic combination, may prompt directional changes.

In modern times, human actions have been an important stimulus to this type of selection. Mankind transforms the environments of many organisms, which rapidly respond to the new environmental challenges through directional selection. A well known example is industrial melanism, the gradual darkening of the wings of many species of moths and butterflies living in woodlands darkened by industrial pollution. The best-investigated case is the peppered moth, *Biston betularia*, of England. Before the industrial revolution, the light form of the peppered moth was well camouflaged among the light-colored lichens that grew on trees around London. Since color variation is known to exist in other moths, a dark form of the peppered moth probably existed, but was never observed because it was easily spotted and eaten by predators. Following the industrial revolution, soot killed the lichens, exposing the dark tree bark below. As a result, the dark or melanic variety of moth which coexisted with the lighter-colored morph increased in number, presumably because these were better hidden or camouflaged from predators. One hundred years after the first dark moth was discovered in 1848, ninety percent of the peppered moths were dark colored. However, the dark form did not become fixed in most populations, possibly because the viability differs among the genotypes, even in the absence of predation. The gene for coloration shows the melanic form is controlled by a dominant allele, while the lighter form is controlled by a recessive allele. In unpolluted regions of western England and Scotland, the dominant allele does not confer a selective advantage to the light recessive moth. The light form of the moth continues to dominate populations in unpolluted areas outside London.

Another common example of directional selection is the spread of antibiotic and pesticide resistance. All chemical insecticides, to a greater or lesser extent, exert a selective pressure upon the insect pests they are intended to control. Therefore, given sufficient time, resistant strains of insects are bound to emerge. The time to resistance depends on a number of factors, including the frequency and nature of resistance genes, pest management strategies, and the relative fitness of the resistant strains relative to the wild type (which is still sensitive to the insecticide in question). Currently, approximately 500 species of insect pest are resistant to one or more common insecticides. This includes pests on important food and fibrer crops, such as cotton, and public health pests, such as disease carrying mosquitoes.

Directional selection on quantitative characters may be quite common in environments that are changeable. One classic is that of selection on bill size in Darwin's finches. The medium ground finch, *Geospiza fortis* lives on the Galapagos islands along with fourteen other finch species. It feeds on the seeds of the plant *Tribulus cistoides*, specializing on the smaller seeds. The health of these bird populations depends on seed production. Seed production, in turn, depends on the arrival of the wet season. During a drought year, in 1977, a very strong directional selection for large birds with large bills was observed. The reason for this was that the average size of the seeds increased, because drought-resistant plants tended to have big seeds. As a result, there was quite a large shift in bill and body size in the next generation, because these characters were heritable in the population. An interesting aspect of this case was that the pattern of the directional selection seemed to change from year to year depending upon the weather. 1985 was a very wet one and there were a lot of small soft seeds that the large-billed individuals are not good at dealing with. During that year the characters positively selected in the dry years were all selected against.

Naturally occurring directional selection on quantitative characters has been detected in the field, but in general it is not long sustained in one direction, and it can reverse in sign from time to time. In the long term, this type of fluctuating selection is likely to maintain genetic variability for the trait, because different character values are favored at different times. Consequently, alleles that decrease, and those that increase the phenotypic trait value, will undergo periods of favorable selection and persist in a population. Over geologic time, directional selection can lead to major changes in morphology and behavior of a population or species. Evolutionary changes that persist in a continuous fashion over long periods of time are known as evolutionary trends. It is thought that directional evolutionary changes increased the cranial capacity of the human lineage from the small brain of *Australopithecus*, human ancestors of three million years ago, which was about five hundred cubic centimeters in volume, to a brain nearly three times as large in modern humans.

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