Evolutionary Biology Today

1. The Domain of Evolutionary Biology

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"For a biologist", wrote Sir Peter Medawar, "the alternative to thinking in evolutionary terms is not to think at all". Yet, at the end of an education in biology in most Indian universities, this is not quite the view of evolutionary biology that one is left with. Evolution is presented summarily, almost as a footnote, rather than as a vital branch of biology providing the conceptual foundation for our modern views about the living world. In this issue of *Resonance*, we remember Stephen Jay Gould, who wrote extensively and eloquently about evolution for a general audience. It seems fitting, then, to also briefly discuss why evolutionary biology is important, not only conceptually but also in terms of practical applications. In this first part of a series of articles on modern evolutionary biology, we examine why the idea of evolution is so important in our intellectual history, and also take a look at the domain of evolutionary biology as a discipline.

Evolution makes its appearance in most Indian biology curricula almost grudgingly, tagged on as an afterthought at the end of one paper or another, summed up in three trite phrases: *overproduction of offspring, struggle for existence*, and *survival of the fittest*. Of course, in zoology curricula one studies the history of the evolution of different animal phyla (and likewise in botany), but of evolution as a dynamic process one learns next to nothing. On the other hand, Theodosius Dobzhansky once described evolutionary biology as the study of the very dynamics of life, and Michael Rose began his 1998 book *Darwin's Spectre* with the words: "A spectre is haunting the modern world, Darwin's Spectre, Darwinism. This spectre has frightened religious ministers, curdled school curricula and left the politically correct ill-at-ease...Alone among modern scientific doctrines, Darwinism

has upset many beyond the academy. It has had enemies on the right and the left, and some states...liquidated Darwinians for their scientific beliefs... Darwin's Spectre won't go away." Why is it that the Darwinian view of evolution occupies such a unique position among major ideas in the intellectual journey of our species from astrological speculations to the present time?

The Idea of Evolution

If we examine the living world with all its many creatures, three aspects of living things stand out: the diversity, the relatedness, and the adaptedness of species. There is a stunningly diverse array of lifeforms inhabiting the earth, from unicells to giant trees, from starfish to snakes, from centipedes to kangaroos, and from seaweeds to humans. Yet, this diversity is not just a random explosion of riotous forms: there are distinct patterns that we recognize. We can clearly see that frogs and toads are more similar to each other than either is to a dog, and also that dogs, toads and frogs resemble each other more than either one of them resembles a butterfly. Thus, we can arrange living organisms in hierarchical groups, with groups lower in the hierarchy containing species that are relatively more similar to one another, and with several such groups together making up larger groups at higher levels of the hierarchy. Indeed, it is because of these hierarchical patterns of similarity that we can have a taxonomy at all. Not only this, we also find that species are typically quite well suited in terms of their morphology, physiology and behaviour to the environments they inhabit, and the lives they lead. Another, fourth aspect of the living world that is apparent if we look around us is that biological systems are full of variation at every hierarchical level of organization. Whether we look at individuals within a population of a species, or different populations of a species in different areas, or different species within a genus, we find variation. No two individuals in a population are identical, and neither are two populations of a species identical. What, then, are we to make of this incredible array of adaptive, hierarchically arranged, biological variation?

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Prior to Darwin, there was no particular explanation for these four attributes of the living world. In most civilizations, there was a tacit acceptance that this was the way things were or happened to be. In the intellectual world of Europe in the 18th and 19th centuries, the dominant view was that God had created the living world in this manner and with these attributes. This may have been a comfortably satisfying view but was in no sense an explanation. There were not even many serious attempts among biologists to discern some general principles or laws shaping the patterns of diversity seen in the living world, even while retaining a belief in a supreme creator, as had been the case in physics with the work of Galileo, Newton and others. Added to this was an intellectual tradition going back to Plato, that underlying the surface of things are their true inner natures or 'ideas' (eidos). In Plato's view, these ideas, or essences, were of greater importance than the variety of ways in which individual objects manifested them. Aristotle, the first great biologist in the European tradition, was a student of Plato and, not surprisingly, applied this point of view to the living world. Thus, in Aristotelian biology, the variations among individuals of a species were unimportant, mere distracting noise about an underlying essence of that species. Aristotle further extended this view to inheritance and postulated that it was the species essence that was transmitted from parents to offspring. Coincidentally, this view of biology also fit in well with the later European tradition of Rational Christianity. As Michael Rose writes in his book *Darwin's Spectre*, "Essences and Supreme Beings go together quite nicely, lending an elevated tone to biology, which after the Renaissance fashioned itself part of natural theology". This Platonic viewpoint has been quite tenacious in its grip upon biologists: even today, when you open a biology textbook and read about the 'archetype' of a species, you are face to face with the ghosts of Aristotle and Plato!

What Darwin's theory of evolution did was to simultaneously provide a coherent and reasonable explanation for the relatedness of species (through the principle of modification by de-

scent), as well as for the adaptedness and diversity of species (through the notions of natural selection and adaptive diversification in the face of competition, respectively). Darwin also clearly recognized that messy variation, not some abstract underlying species essence, is the true face of biological reality. Indeed, the notion of natural selection is predicated upon the existence of heritable variation in biological attributes. In fact, Darwin's main contribution to biology was not to suggest that evolution had occurred – the idea of evolution was already around thanks to Lamarck and a few others – but to provide a mechanism whereby adaptive evolution could take place, and to marshal evidence and arguments in favour of this mechanism. The one missing link in Darwin's theory of evolution by natural selection was a mechanism of inheritance that would tend to maintain genetic variants in a population over generations. Mendel's work provided this link, and Fisher and Wright welded the laws of genetics and the notion of natural selection into a comprehensive theory of how evolution works (see *Resonance* Vol. 2, No. 9, pp. 27-31).

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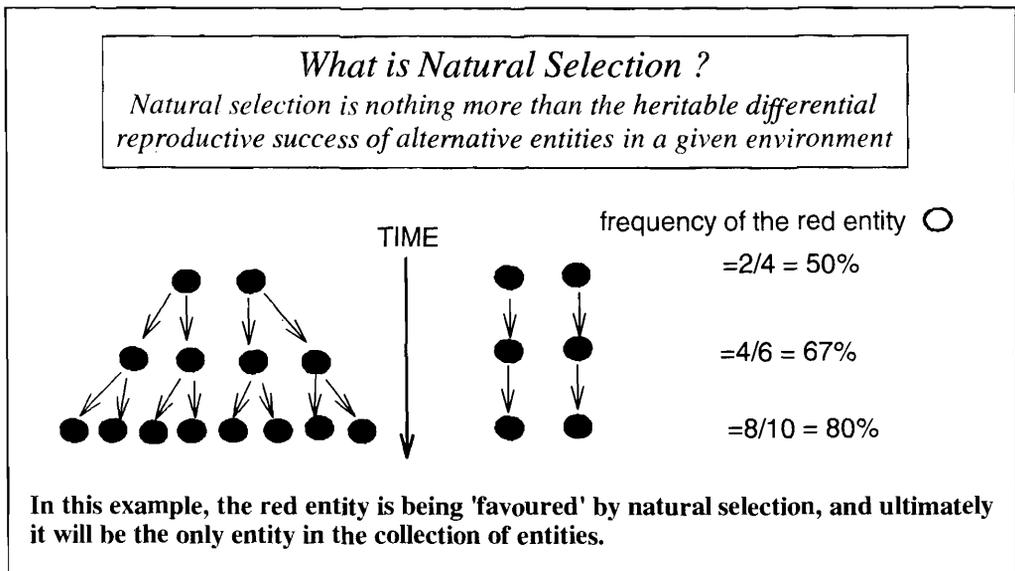## Adaptive Evolution and Natural Selection

We are all familiar with the phrase '*survival of the fittest*' as a pithy depiction of Darwin's theory. This phrase, coined by Darwin's contemporary Herbert Spencer, is singularly unfortunate as it conveys the impression of a violent physical struggle among organisms with the more powerful ones killing off those weaker than themselves. The point is that survival here implies long term persistence over evolutionary time, not life and death, and fitness implies not physical prowess but the relative ability to produce offspring. A much more accurate and equally concise description of natural selection is '*heritable differential reproductive success*'. What does this imply?

Consider any entity that can reproduce, or make copies of itself. Now consider that different individual entities vary in their relative ability to make copies of themselves. Assume, further, that the ability to make a particular number of copies is trans-

mitted (inherited) to the copies made. Then, after many rounds of copy making (reproduction), the type of entity that makes more copies each time will outnumber others (*Figure* 1). This is all that is required for natural selection to take place. Indeed, if these conditions are satisfied, natural selection among these entities is occurring by definition, and we would say, in context of *Figure* 1, that selection is favouring the red entity. Note that this phrase is just a convenient shorthand: selection is not a particular force favouring anything. All that is happening is that the red entity, by reproducing at a greater rate than the blue, comes to become more abundant in the collection of entities over time. That's it! That is natural selection.

In the preceding paragraph, we were speaking of entities rather than individual organisms. Most often, in biological evolution, the entities among which selection is occurring are individual

Figure 1. A schematic depiction of the basic notion of natural selection. Imagine a collection of two types of entities, red and blue. Initially, the collection consists of two each of the red and blue entities. Both kinds of entities last for one unit of time, and then disappear, after having made copies of themselves. They differ in the efficiency of making copies: the red entity makes two copies of itself at the end of one time unit, whereas the blue entity makes only one copy of itself. The figure shows how, as a consequence of the difference in the rate at which they make copies, the red entities come to outnumber the blue entities after a while. This is natural selection.

What is Natural Selection ?

Natural selection is nothing more than the heritable differential reproductive success of alternative entities in a given environment

TIME

frequency of the red entity ○

=2/4 = 50%

=4/6 = 67%

=8/10 = 80%

In this example, the red entity is being 'favoured' by natural selection, and ultimately it will be the only entity in the collection of entities.

organisms, although there are exceptions to this. However, as Fisher pointed out in the 1930s, and as genetic algorithms today demonstrate, natural selection is not constrained to the living world. Natural selection will operate on any entities, as long as there are heritable differences in the rate at which the individual entities make copies of themselves. This is the core mechanism of adaptive evolution. It is simple, indeed almost simplistic, but the subtlety lies in the mechanistic details. If we consider selection acting on individual organisms, the unit of selection is the individual, but the unit of evolution is the population. This is because an individual cannot change over evolutionary time: it merely dies. What changes over time is the composition of the population. As generations go by, the population consists of a larger proportion of individuals that are relatively better off at coping with, and reproducing in, the particular environment occupied by the population. This is what is usually meant by adaptive evolution: the mean Darwinian fitness of the population tends to increase over generations. This sort of adaptive evolution that fine tunes the adaptedness of a population to its environment is often called microevolution, as contrasted with macroevolution or the origin of new species or higher taxa. In the rest of this series of articles, I will use evolution to mean microevolution, unless otherwise specified.

The Domain of Evolution

The process of adaptive evolution can be viewed by analogy to an example from basic physics. We all learn that when a force acts upon a body, the body moves along a certain trajectory through space and that the trajectory taken by the body depends not only upon the force but also upon the structure of the body. We also learn that multiple forces can be resolved into a single net force. Applying this analogy to evolution, consider a population as the body. Imagine a space whose axes are the various attributes of that species – this is the phenotypic space, and the population can be represented as a point in this space based upon its mean phenotype for all the different traits that constitute the axes of the space. When the population changes in its

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attributes, therefore, we can think of the change as the population moving to another point in this n-dimensional phenotypic space. If we track these changes over generations, we can construct an evolutionary trajectory of this population that shows us exactly how its overall mean phenotype changed through time. The force acting on this population is the force of natural selection; this is nothing more or less than a resolution of the ecology of that species. As a result of this force, the body takes a particular evolutionary trajectory through phenotypic space, and the nature of the trajectory is determined by the force of natural selection, as well as the structure of the body, and also by chance events (*Figure* 2). By the structure of the body, we mean certain genetic attributes of the population, something formally called *the genetic architecture of fitness*, a concept we will discuss in detail in subsequent articles. This view of adaptive evolution,

Figure 2. A simplistic view of adaptive evolution. The evolutionary trajectory of a population can be viewed as analogous to the trajectory of a body upon which a force acts. The evolutionary trajectory records how the phenotypic composition (and, therefore, the mean phenotype) of the population changes over time, and is the result of an interaction between the force of natural selection and the structure of the population. The force of natural selection is the resolution of the entire ecology of the organism into a net statement about which phenotypes are better able to survive and reproduce, while the structure of the population refers primarily to the way in which different traits relevant to fitness in that environment are genetically correlated with each other (modified from Fig. 1 in A Joshi 2000, J. Indian Inst. Sci., 80: 25-37).
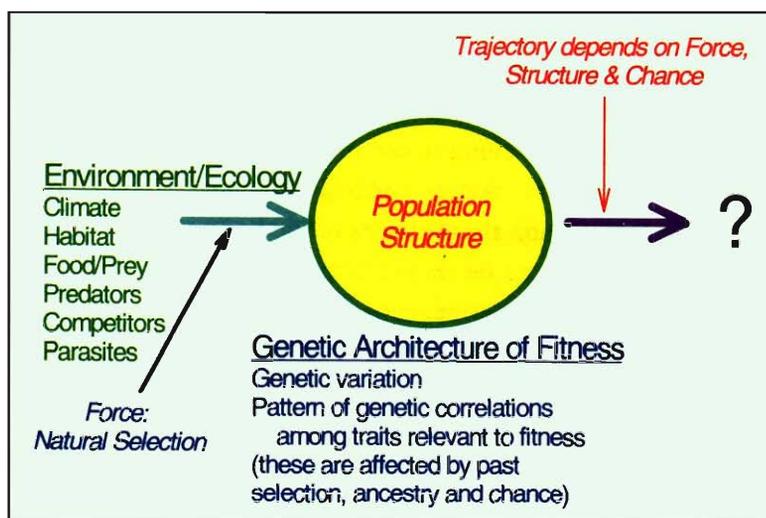
however, is a somewhat simplified one. We say that natural selection is acting on the population and that, as a consequence, the mean phenotype of the population is changing over generations. However, the phenotype does not transmit itself to subsequent generations; that is done by the underlying hereditary endowment, or the genotype. Thus, there are three aspects of living systems to consider when thinking about their evolution: the genotype, the phenotype, and the environment (*Figure* 3).

If we look at the bottom of *Figure* 3, we have the meiosis-fertilization cycle that characterizes the haploid-diploid alternation of generations characteristic of most living organisms. There are two aspects of this process of transmission of genetic material that need to be noted. First, diploid genotypes do not get transmitted to the next generation. Meiosis chops up multilocus diploid genotypes in two important ways that have evolutionary consequences. During meiosis alleles at the same locus on different chromosomes in an individual get separated due to the production of haploid gametes from diploid precursors. Similarly, alleles on different loci on the same chromosome can get separated due to crossing over. Thus, meiosis shuffles up the

Figure 3. A more detailed view of evolution in living systems (the depiction is with diploid organisms in mind, but the general issues are the same for haploids as well). Below the dotted brown line is the genetic domain, and the dark violet circle represents the haploid-diploid-haploid cycling of genetic material through the alternation of meiosis and fusion. The blue arrows in the centre of the figure represent influences that play a role in the lifetime of an individual, whereas the brown arrows to the right of the figure represent influences on the evolution of the population of individuals.
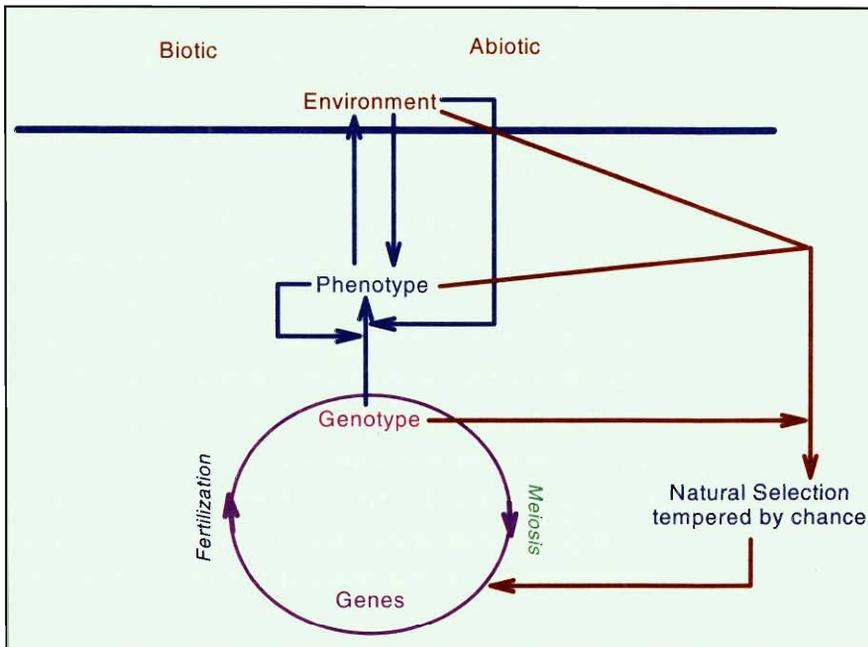
Meiosis shuffles up the multi-locus diploid genotype along both axes: across chromosomes, as well as within chromosomes. What is then transmitted to the next generation are newly shuffled combinations of alleles at various loci, reconstituted into multi-locus diploid genotypes by fertilization.

multi-locus diploid genotype along both axes: across chromosomes, as well as within chromosomes. What is then transmitted to the next generation are newly shuffled combinations of alleles at various loci, reconstituted into multi-locus diploid genotypes by fertilization. Understanding and quantifying the consequences of this shuffling for the genetic composition of populations is the domain of population genetics. The second important aspect of transmission of genetic material is that the phenotype is required. Nucleic acids do not replicate themselves without an elaborate machinery. In most cases, this machinery is embedded within an even more elaborate organism, and the cycle of meiosis and fertilization occurs within a complex lifeform that needs to feed (or photosynthesize), avoid or defend itself against other species, find a mate, etc.

Thus, genotypes direct the formation of phenotypes (the blue arrow in the middle of *Figure* 3). The production of the phenotype is affected both by the phenotype itself, and by the environment. For example, proteins already in the fertilized egg can affect the way in which genes early in development are switched on, and environmental conditions can do the same at practically any stage of development. The central arrow in *Figure* 3 represents the domain of developmental biology: the generation of the phenotype under the direction of the genotype. Continuing towards the upper part of *Figure* 3, the phenotype can be further influenced by the environment and can, in turn, influence the environment. The environment itself, of course, consists both of the physical environment as well as other individuals of the same or different species. Physiology, behaviour, etc. occupy the middle part of the figure in this schematic. They constitute what the phenotype 'does' and 'how' it does it. However, whatever an organism does is not done in a vacuum: it is done in a specific physical and biological context. Therefore, behaviour and physiology are best understood in the context of the organism's environment, and this interface of phenotype and environment (the blue solid line in *Figure* 3) is the domain of ecology.

Now consider the longer term consequences of the interaction between a organism's phenotype and the environment. Some individual phenotypes, by virtue of their underlying genotype and environmental conditions during their lifetime, are better able to make a living and find a mate and produce offspring in the particular environment they experience, compared to other contemporaneous phenotypes. Thus, their genotypes – or rather, the alleles making up their genotypes – are transmitted to the next generation to a greater degree than those of the other phenotypes. This is natural selection, depicted in *Figure* 3 by the brown arrows leading from environment and phenotype to the cycle of meiosis and fertilization. Sometimes purely genetic considerations (the genetic architecture of fitness, meiotic drive, etc.) can also affect the transmission of alleles to the next generation: that is the brown arrow leading from 'genotype' to 'natural selection' in *Figure* 3. We will deal with some of these issues in detail in subsequent articles.

Conclusion

I hope that this article has left you, the reader, with some feeling for the domain of evolutionary biology, and for why the idea of evolution is considered one of the major intellectual achievements of humankind. As the depiction in *Figure* 3 suggests, evolution in its broadest sense is concerned with life itself: all biology is evolution. This is the sense in which Dobzhansky called evolution the study of the very dynamics of life. No other idea in biology has the sweep and the scope of evolution which encompasses both the diverse and striking particularities of life, as well as the equally impressive similarities among lifeforms. In subsequent articles in this series, we will discuss in greater detail some of the specific kinds of questions addressed by evolutionary biologists and the tools and techniques they use. In addition, we will also discuss some of the important applications of evolutionary biology to agriculture, medicine, conservation and to the way in which we think about human history and society.

Suggested Reading

[1] M R Rose, *Darwin's Spectre: Evolutionary Biology in the Modern World*, Princeton University Press, Princeton, USA, 1998.

[2] R Dawkins, *The Selfish Gene*, Oxford University Press, New York, USA, 1976.

[3] S J Gould, *The Panda's Thumb*, W W Norton & Co., New York, USA, 1982.

[4] F J Ayala, Theodosius Dobzhansky: a man for all seasons, *Resonance*, Vol. 5, No.10, pp. 48-60, 2000.

[5] A Joshi, Sir. R A Fisher and the evolution of genetics, *Resonance*, Vol.2, No.9, pp. 27-31, 1997.

[6] A Joshi, Sewall Wright: A life in evolution, *Resonance*, Vol. 4, No.12, pp. 54-65, 1999.

[7] S C Stearns and R F Hoekstra, *Evolution: An Introduction*, Oxford University Press, Oxford, UK, 2000.

[8] Special Section on Evolutionary Ecology, *Current Science*, Vol.72, No.12, pp. 923-956, 1997.

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