

# On directional and non-directional evolution by natural selection

Lars Witting

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## Abstract

Since Darwin evolutionists have agreed that evolution by natural selection is a non-directional historical process. However, a new theory suggests that life-history evolution resembles a deterministically unfolding process where simple self-replicators in stable environments with plentiful resources automatically evolve toward the complex organisms on Earth. The arguments in favour of the old and new hypotheses are explained, and a discussion aims at identifying the scales at which the two hypotheses apply.

## Introduction

There seems to be a new situation in evolutionary biology. Since Darwin we have learned that evolution by natural selection is historical in the way that features shared by different organisms do not represent universal laws of selection, but instead useful mutations that are passed down through the phylogenetic tree. A new theory (Witting, 1997), however, suggests that evolution by natural selection is a deterministically unfolding process where a simple self-replicator in a stable and favourable environment automatically evolves toward the complex organisms on Earth. We have now, for the first time, a deductive theory of natural selection that suggests that the classical interpretation of historical evolution is too limited.

The purpose of this talk is not to describe the proposed theory in detail. This is done by Witting (1997a) who performs the mathematical deductions, and by Witting (1997b) who gives a summary. The purpose is instead to describe and discuss the theoretical background that makes it possible to conclude whether evolution by natural selection is inherently directional or not.

## The classical view

Let me first introduce the classical view on evolution by natural selection by presenting a few quotations from recent publications of well-established evolutionists:

“Modern biology sees itself as a deeply historical science” where “Shared features among organisms . . . are seen not as expressions of underlying law, but as contingent useful accidents passed down through progeny” – – Kauffman (1995:22)

“selection is an optimization process, but one of a very special kind. It is neither teleologically programmed nor controlled by any law, but is entirely opportunistic.”  
– – Mayr (1988:105)

“On the theoretical side, there is no reason why evolution by natural selection should lead to an increase in complexity” – – Maynard Smith & Szathmary (1995:4)

“the term evolution in its original sense of an unfolding or development, analogous to the development of an individual animal, is misleading” – – Salthe (1989)

“if we could rewind the tape of evolutionary history to the remote past and play it again, it would turn out entirely different.” – – Gould (1989:48)

“Might there be somewhere a planet on which the biota arises and becomes more complex deterministically?” – – Williams (1992:8)

These statements illustrate the traditional view: that evolution by natural selection is dominated by opportunity and chance, and not by a few laws of selection that explain the observed structuring of organic matter. The particular solution whereby a given organism evolves a trait by natural selection will always, at least to some degree, depend on opportunity and chance. As we all know there have been plenty of different solutions to the evolution of eyes. But this degree of historicity and randomness is not special to evolutionary biology. It applies also to many physical processes. From plate tectonics we may predict the occurrence of mountains, but the specific shape of the mountain is given by chance and opportunity and thus it remains largely unpredictable.

Apart from the historicity associated with the particular solution to the evolution of a given trait, the quotations describe another level of historicity where it is hypothesised that natural selection is lacking universal laws, or forces, that explain the overall structuring of organic matter. The evolutionary process is seen to have no overall direction so that organic matter contains no inherent drive towards complexity. This workshop deals with this latter form of historical and non-directional evolution, examining whether the classical hypothesis is likely to hold, or whether evolution by natural selection is better described as a deterministic directional process. And it is at this level that we shall understand the theory that I have proposed a theory that suggests that the overall structuring of organic matter be determined mainly by three different forces of selection. One arises from the exploitation of the resource, a second from the action of density dependent competitive interactions, and a third from an intrinsic optimisation of the phenotype.

## **Empirical facts**

Before we turn to the theoretical discussions on directional versus non-directional natural selection, let us examine if the empirical facts that are available to us at the present time can help us to determine whether the classical view is correct, or whether evolution by natural selection is inherently directional.

From empirical evidence we know that evolution on Earth have included a directional change where simple self-replicators have evolved into large multi-cellular organisms with high metabolic rates and complex behavioural interactions. It is also suggested that as the body mass increases the major life-history traits evolve in concordance with the exponents of the body mass allometries. A comparison between prokaryotes and the higher eukaryotes suggests furthermore that the transition from a negligible to a relatively large body mass is associated with an evolutionary transition from a haploid organism with no soma, no senescence, and no sexual reproduction, to a diploid organisms with soma, senescence, and sexual reproduction between a male and a female. In a few special cases, mostly in insects, there has been an additional transition to eusocial communities, a transition that in some instances seems to coincide with a transition from a diploid to a haplodiploid genome.

Superimposed upon this evolutionary direction there has been a large amount of diversification illustrating that many organisms have been left aside from the directional increase, and that many organisms have shown evolution in the opposite direction experiencing, e.g., an evolutionary decline in mass. Although it cannot be questioned that an overall increase has occurred, the diversification shows that the evolutionary increase is not so general that it applies to all organisms.

The diversification is not an argument against directional natural selection. This is because natural selection is only expected to have an overall direction if the environment is stable. If the environment varies we may actually expect an overall direction and diversification induced by environmental fluctuations and by environmental differentiation among organisms. But the observed direction may also reflect nothing but chance and opportunity. To prove that evolution in natural organisms is directional we need to produce parallel evolutionary trajectories in independent experiments, or to discover evolution on other planets that resemble evolution on earth. As none of these options are yet available it is most natural to approach the concept of deterministic directional evolution by theoretical considerations.

## Directional and non-directional natural selection

Consider how the concepts of non-directional (historical) and directional (deterministic) evolution by natural selection can be defined. If natural selection is non-directional it follows that long-term evolutionary is shaped by chance and opportunity. Such a process is possible if selection on a relatively large set of traits is so weak that the evolutionary determinants of these traits are given not by underlying laws of selection but instead by random drift. Given that many traits arise by random drift they may subsequently induce selection on other traits. In this way the latter traits can be selected for by a historical form of selection which arises from the physiological and phylogenetic constraints induced by the traits that evolve by random drift.

This scenario of historically induced selection can be described mathematically in the following way. Let  $\mathbf{P}$  be the set of traits that contain all the phenotypic traits that we consider. Let  $\mathbf{F}$  be the fundamental traits that arise by chance and opportunity, and let  $\mathbf{D}$  be the derived traits that evolve by the selection pressure imposed by the constraints of the fundamental traits. Hence,  $\mathbf{P} = \mathbf{F} \cup \mathbf{D}$ . Then, the fraction of the phenotype that is determined by natural selection is

$$\mathbf{D} = f(\mathbf{F}) \tag{1}$$

where  $f$  is the selection function that arise from the constraints of the fundamental traits  $\mathbf{F}$ . This type of selection is possible as long the fundamental traits  $\mathbf{F}$  are selectively neutral. If instead there is strong selection against the fundamental traits, then the evolutionary prediction of eqn (1) will fail because it is evolutionarily unstable in  $\mathbf{F}$ .

If instead evolution by natural selection is deterministically directional we expect that universal laws of selection give the long-term trajectory and that the phenotype is an unfolding function of time. Using the same notation, this form of selection can be described mathematically as

$$\mathbf{P} = f(t) \tag{2}$$

where the selection function  $f$  defines the selection pressure as a function of time ( $t$ ). In this case there may also be some components of the phenotype that is defined by a historical form of selection that resembles that of equation one. But for the situation with directional selection the fundamental traits in eqn (1) will be given by the deterministic formula of eqn (2), and not by chance and opportunity as expected for the case with non-directional evolution.

## Dimensionality of evolutionary optima

Another way to describe the difference between historical and deterministic selection is to focus on the dimensionality of the optima (equilibria) in the two theories. Here a dimension refers to a trait that has evolved by the selection function of the model. Thus the dimensionality refers to the number of phenotypic traits that are in equilibrium at the theoretical optimum, instead of being given as an assumption to the model. If a trait is given by assumption it resembles one of the fundamental traits in eqn (1), implying that a historical model contains explicit phenotypic assumptions whereas a deterministic model does not.

In classical life-history theory it is often the custom to operate with single-dimensional optima. For example, in the Fisherian sex ratio theory the sex ratio is the single trait that has an evolutionary optimum, and this optimum depends on at least four phenotypic assumptions. These are the existence of males, the ploidy level of the genome, the existence of sexual reproduction, and the degree of local mating. If instead we have a model that explains the presence of males, the sex ratio, and the degree of local mating from the ploidy level of the genome and the presence of sexual reproduction, then, we would have a three-dimensional optimum.

The best we can do with any set of traits is to make a model that has an all-dimensional optimum (ADO) where all the traits in the set are explained without making explicit assumptions with respect to the other traits that have evolved by natural selection. For the sex ratio example the ADO model is reached when the presence of males, the sex ratio, the presence of sexual reproduction, the ploidy level of the genome, and the degree of local mating have been explained independently of other phenotypic traits.

An ADO model does usually not provide us with an explanation for the evolutionary determinants of the complete organism. For this we need a complete-dimensional optimum (CDO) that has evolutionary optima in all the dimensions included in the phenotype of the organism. Although CDOs most probably cannot be obtained even for the simplest organisms they provide us with the ultimate goal in theoretical evolutionary biology. To approach this goal we can proceed in successive steps making ADO models that include an increasing number of traits.

These definitions have illustrated some basic differences between historical and deterministic selection. We may then proceed by considering how the classical life-history theory and the theory that I have proposed fit into the definitions of respectively historical and directional natural selection.

## Classical life-history theory

On the theoretical side the classical theory is described by the life-history theory that is reviewed by Roff (1992), Stearns (1992), Charnov (1993), Bulmer (1994), and Charlesworth (1994). This theory is generally based on the assumption of constant relative fitnesses and it tends to disregard the effects of competitive interactions. On a first examination the classical life-history theory seems to resemble the definition of historical natural selection, where the predicted phenotypes are given by selection that arises from phenotypic constraints.

The Fisherian sex ratio model described above is one example of this. Other examples are Roff's (1981) model where the body mass evolves from a proportional relation that exists between the reproductive rate and body mass. Lack's (1947) clutch size, where the reproductive rate evolves from a trade-off between the reproductive rate and offspring or parent survival. William's (1957) theory of senescence, where senescence evolves from the presence of a soma. And Hamilton's (1964) kin selection theory where it is the eusocial colony that evolves from kin selection and a haplodiploid genome.

## Limits to classical theory

As I mentioned in connection with the definitions of historical and deterministic selection, the hypothesis of historical evolution holds only if the phenotypic assumptions are evolutionarily stable. But under the action of the selection pressure defined by the classical life-history theory there is generally strong selection against the phenotypic assumptions. For example, when we allow for selection on the phenotypic assumptions in the classical theory, it follows that the framework behind Roff's theory predicts a continuous decline in body mass because the resource that is contained in the mass is selected out into numerical replication. And the model behind Lack's clutch size predicts a continuous increase in the reproductive rate because there is selection for a continuous decline in the trade-off between reproduction and survival. Likewise, the Fisherian sex ratio theory predicts extremely female biased sex ratios because the two-fold cost of the male selects against the male individual. In general, as describe by Witting (1997), all the classical predictions tend to collapse to that of simple self-replicators whenever we allow for selection on the phenotypic assumptions upon which the classical predictions are based.

Actually, instead of supporting the classical hypothesis of historical evolution, it follows that the classical life-history theory supports the hypothesis of directional evolution. Unfortunately though the predicted direction toward simple self-replicators is diametrically opposite to the evolutionary direction observed on Earth. So in conclusion it appears that the classical life-history theory is failing altogether at an evolutionary scale where we are interested in the evolutionary stability of the predicted equilibria. For me this is a major and very serious problem, not only for the classical life-history theory, but also for the classical hypothesis of historical and non-directional evolution.

## Possible solutions

Due to the evolutionary instability of the equilibria of the classical life-history theory we are faced with the problem of obtaining evolutionary equilibria that differ from simple self-replicators. Dealing with the evolution of the major life-histories it does not seem that we can apply the classical hypothesis of non-directional evolution. This is because these life-history characters are closely connected with the fitness of the organism and, thus, we do not expect that a subset of these characters evolve by chance and opportunity alone. We expect instead that all major life-histories are determined more or less exclusively by natural selection. This implies that these characters most likely are situated close to an all dimensional optimum, if not they are continuously evolving towards an ever moving optimum.

The overall task is to construct a theory that allows for the observed diversity among natural species and predicts phenotypes that are evolutionarily optimal in all dimensions. One way to obtain this result is by the use of selection that is directional in stable environments. The diversity among organisms can then be explained by differences in environmental conditions and by differences in the degree to which the different organisms have evolved along the dimension of directional selection.

## Proposed life-history theory

The theory proposed by Witting (1997) conforms to directional evolution in the way that it describes evolution by natural selection as an optimisation process that is not constrained by phenotypic contains. This means that I have aimed at a theory where the only allowable constraints are the process of self-replication (i.e., the definition of life), and physical and ecological constraints that cannot evolve by natural selection. The essential idea is then to deduce the major evolutionary trajectory from these first principles.

From these first principles we expect two different forms of selection. The first force arises from the exploitation of the resource where, other things being equal, it is the individual with the highest exploitation efficiency that can have the highest fitness because it has more resource available for reproduction, survival, and/or competitive quality. The second force is the selection pressure that arises from the density dependent competitive interactions that are unavoidable among the individuals in natural populations.

These two forces of selection play two distinctively different roles. The selection pressure of exploitation induces a direction to the evolutionary process, where the organism experiences an increase in energetic quality, i.e., an increase in the amount of resource or energy that it can assimilate from the environment. The selection pressure of density dependent competitive interactions, on the other hand, can explain the allocation of the assimilated resource among the different life-history traits. And when the two forces are combined we obtain the phenotypic transitions that are known from the major evolutionary trajectory.

Together the selection pressures of exploitation and density dependent competitive interactions define the limited or special version of the proposed theory. The theory has also a general version that includes a third force of selection that arises from an intrinsic optimisation of the phenotype. This latter version can be seen as an integration between the classical life-history theory and the special version of the proposed theory, and it generates the equilibria of the classical life-history theory in an improved form where they are evolutionarily stable. These new equilibria, however, differ from the original equilibria in the sense that they explain not only the evolution of the original predictions but also the evolution of the phenotypic assumptions that underlie the classical predictions. Another difference is an almost complete change in the evolutionary causality that generates the evolutionary stability of the predicted equilibria. For example, where the traditional version of Lack's clutch size explains the optimal rate of reproduction from a trade-off between reproduction and survival, it follows that the new version explains the trade-off from the optimal rate of reproduction.

## Scales of evolution

The conclusion seems to be that there is no evidence that the classical hypothesis of non-directional evolution holds at the scale of the major life-histories. In fact there seems to be more evidence in favour of the hypothesis that a directional form of natural selection determines these life-histories. This conclusion is reached because at present we have a selection theory predicting directional evolution, while on the theoretical side there is no reason to expect that the major life-histories evolve by a historical form of natural selection.

Although it seems that historicity have played only a minor role in determining the major evolutionary trajectory, the concept of historical evolution still holds at smaller scales. Empirically we know that evolution is historical to the degree that all organisms do not proceed along a single evolutionary trajectory. Depending on the trait in question there is a tremendous amount of variation among natural species, and the evolutionary process is better described as a tree than as a single lineage. It is also clear that many closely related species look more or less the same because of shared phylogenetic constraints, and not because of a directional form of selection. Especially when we deal with traits that are not strongly associated with fitness the historical approach of chance and opportunity is likely to be more correct than the idea of directional evolution. So even if life-history evolution is directional we do not expect to find elephants on other planets. Instead we may expect large and intelligent mobile organisms with senescence, soma, and sexual reproduction between males and females. In this way the historical view of natural selection is easily integrated with the directional view.

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