

Conclusions from a general theory of evolution

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Abstract

During evolution on Earth there has been a directional change where self-replicating molecules have evolved into large multi-cellular organisms with high metabolic rates and complex behavioural interactions. Associated with this increase there has been a transition from an asomatic, non-senescing, haploid, and asexually reproducing organism to a somatic, senescing, diploid, and sexually reproducing organism. In a few cases there has been an additional transition into eusocial communities.

Despite this directional increase in complexity evolutionists since Darwin have agreed that evolution by natural selection is historical and non-directional. However, Witting (1997) develop a new theory suggesting for the first time that evolution by natural selection is inherently directional in the directions mentioned above. The theory developed also provides the first explanation for the body mass allometries that describe the major life-histories across mobile organisms, and it provides a single-species mechanism for the population cycles that have fascinated ecologists for decades.

This article is a summary describing some of the major conclusions reached by Witting (1997), but it does not describe the logic that leads to these conclusions. In order to understand the proposed theory in detail you will have to consult the original text.

Introduction

Witting (1997) proposes a new and general theory of evolution by natural selection, and he analyses whether the phenotypic patterns within and among natural organisms can be evolutionarily explained by the proposed theory and/or by the classical theory of evolution by natural selection. This latter theory arose from the ideas laid down by Fisher (1930), and since then it has grown into a mature theory that covers the evolution of the major traits in natural organism. For detailed reviews of the classical theory see Roff (1992), Stearns (1992), Charnov (1993), Andersson (1994), Bulmer (1994), Charlesworth (1994), and Crozier & Pamilo (1996).

The classical theory is based on the implicit assumption that competition is purely exploitative, and the classical predictions tend to fail on an evolutionary scale because they depend on phenotypic assumptions that are evolutionarily unstable. For example, to predict an even sex ratio it is traditionally assumed that males and sexual reproduction exist, and that the genome is diploid or haplodiploid. But according to the selection pressure of the classical sex ratio theory we actually predict that males and sexual reproduction are absent and that the genome is haploid, and consequently we predict also the absence of sex ratios.

Witting's theory includes interference competition in the form of density dependent competitive interactions, and the predictions in this theory tend to hold on an evolutionary scale

because the predictions are evolutionarily stable in the sense that they do not depend on phenotypic assumptions. For example, an even sex ratio is predicted in large-bodied mobile organisms independently of the traditional assumptions.

Another essential difference between the two theories is the way the selection pressure is propagated through the population. In general, the selection pressure is propagated in opposite directions in the two theories. For example, where in the classical theory the selection pressure on the sex ratio depends upon the ploidy level of the genome, in Witting's theory it is the selection pressure on the ploidy level that depends upon the sex ratio.

Another difference between the two theories is that the classical theory suggests that there is no reason why evolution by natural selection should lead to a continuous increase in the complexity of natural organisms, while Witting's theory suggests a directional change where self-replicating molecules evolve into large multi-cellular organisms with high metabolic rates and complex behavioural interactions. Associated with this increase the theory predicts a transition from an asomatic, non-senescent, haploid, and asexually reproducing organism (like viruses and prokaryotes) to a somatic, senescent, diploid, and sexually reproducing organism (like the higher eukaryotes). In a few special cases there is an additional transition into the two different forms of eusociality that we know from respectively termites and ants/bees.

Hutchinson's rule

One of the most clear patterns in natural communities is Hutchinson's rule (Hutchinson, 1959), that two strongly competing species can coexist if their weight ratio is higher than two. Hutchinson's rule was never explained theoretically, and according to classical theory the first law on the assembly of natural species is the Volterra-Gause principle that competitive exclusion inevitably takes place among species that occupy similar niches. The Volterra-Gause principle is, though, basically wrong because it is based on the invalid assumption that competition is purely exploitative (e.g., Schoener, 1976). Also in Witting (1997) it is shown that Hutchinson's rule follows from the regularities by which inter-specific interference partitions the resource among competing species.

Evolution of basic traits

Body mass

According to the classical theory a large body mass evolves from the proportional relationship that often exists between reproduction and body mass within a species (Roff, 1981). This hypothesis has been confirmed on a local scale where demographic models are fitted to empirical evidence within a species, but it fails on an evolutionary scale where it predicts only the evolution of a negligible body mass.

If to the classical framework we add the action of density dependent competitive interactions, then a large body mass will evolve by the density dependence in the number of competitive interactions and the relation that large-bodied individuals can dominate small-bodied individuals during competitive encounters. It also follows that the proportional relationship between reproduction and body mass evolves from ecological constraints, instead of being the intrinsic constraint that defines the selection pressure on body mass as traditionally thought.

The body mass that evolves by density dependent competitive interactions behaves in resemblance with general observations. For example, the body mass is inversely related to the rate of mortality, as it is observed in guppies (Reznick *et al.*, 1996). It is positively related to the production in the resource, which is in agreement with the observations made by McNab (1971) and Geist (1986) in relation to Bergmann's rule. The predicted body mass also behaves

in resemblance with the island rule (Foster, 1964) that large animals generally are smaller on islands than on mainlands while the opposite is true for small animals.

Reproduction

The classical theory on the evolution of the reproductive rate is Lack's clutch size (Lack, 1947), where the reproductive rate evolves from a trade-off that exists between reproduction and either offspring or parent survival. This hypothesis has been confirmed on a local scale where demographic models are fitted to the empirical evidence within a species, but it fails on an evolutionary scale, where it predicts a continuous increase in the reproductive rate.

The classical prediction of unlimited reproduction is in contrast to the hypothesis of selection by density dependent competitive interactions, which predicts that the reproductive rate is balanced against the ecological constraints that determine the bias in the access to resource among the individuals within a species. Among other things, this balance implies that poikilotherm vertebrates reproduce at a higher rate than homoiotherm vertebrates, and that the maximal rate of reproduction is balanced against the level of extrinsic mortality. These predictions are confirmed by empirical evidence, and they are not easily obtained from the classical framework. Also, in relation to the original proposal of Lack, the evolutionary causality is changed around so that it is the physiological trade-off between reproduction and survival that evolves from the optimal value of the intrinsic growth rate. Finally, the new prediction is evolutionarily stable, while Lack's prediction is evolutionarily unstable.

Body mass allometries

During this century the major life-histories across natural species have been empirically established as allometric relationships, which describe the various traits as power functions of body mass (reviewed by Calder, 1984; Peters, 1983; Reiss, 1989). It is generally agreed that the rounded exponents of the power functions are $3/4$ for the metabolic rate, $1/4$ for lifespan, $1/4$ for the level of social behaviour, $-1/4$ for the intrinsic growth rate, $-3/4$ for the population density, 1 for the home-range area, 0 for the resource consumed by a population, and 0 for maximal lifetime reproduction. While a number of explanations have been proposed for these relations it is generally agreed that no single one is convincing.

However, in Witting (1995, 1997) it is shown that the empirically estimated exponents can be explained by the ecological constraints associated with a foraging process that is optimised by natural selection. The most essential constraints are the number of competitive encounters per individual and foraging self-inhibition, i.e., the degree to which an individual's exploitation of the resource inhibits the foraging of that individual. The regulation of the foraging efficiency by these two processes are counteractive, so that there is an intermediate optimum from which it is possible to deduce the allometric exponents. According to this deduction the $1/4$ and $3/4$ exponents apply to organisms that forage in two dimensions, whereas the expected exponents are $1/6$ and $5/6$ among organisms that forage in three dimensions. The two-dimensional exponents are confirmed by terrestrial organisms, and the three-dimensional exponents generally apply to pelagic organisms.

The evolutionary direction

According to the classical theory of evolution "there is no reason why evolution by natural selection should lead to an increase in complexity" (Maynard Smith & Szathmary, 1995:4). Instead, on an evolutionary scale the classical theory predicts evolution in the opposite direction toward

a self-replicating molecule, a prediction that obviously is paradoxical in relation to evolution on Earth.

If, instead, we focus on selection by density dependent competitive interactions and combine this framework with selection on the individuals' ability to exploit the resource, then we predict a directional change where self-replicating molecules evolve into large organisms with high metabolic rates and complex behavioural interactions. Moreover, if there is no immediate constraints to the exploitation efficiency this increase is expected to occur at an exponential rate. As described in further detail below, associated with the increase in body mass the theory predicts a transition from an asomatic, non-senescing, haploid, and asexually reproducing organism (like viruses and prokaryotes) into a somatic, senescing, diploid, and sexually reproducing organism (like the higher eukaryotes). Finally, when the body mass is upward constrained there may be an additional transition into a eusocial colony.

The steady increase in complexity depends on the assumption that the abiotic and biotic factors extrinsic to the population are constant. If, instead, the primary production is declining the increase may reverse to a decline, and there may even be a mass extinction that will eliminate predominantly the larger species while the remaining species tend to dwarf in size. This pattern of dwarfing and extinction is well-known from the fossil record, and if the primary production continues to decline all species are expected to evolve toward self-replicating molecules. In other words, the predicted evolutionary process is reversible with the particular direction being defined by environmental conditions.

Evolution of derived traits

Senescence and soma

According to the classical theory senescence evolves from a somatic tissue from which no part is passed on in either sexual or asexual reproduction (Williams, 1957). This hypothesis coincides with the presence of senescence in the large-bodied eukaryotes that have a soma, and its absence in the small-bodied prokaryotes that have no soma. But the classical theory fails on an evolutionary scale because it does not explain why the higher eukaryotes have a soma when prokaryotes do not.

Witting (1997) developed the alternative hypothesis that the soma is the trait through which senescence is expressed. When this hypothesis is combined with selection by density dependent competitive interactions it follows that senescence and soma are unlikely to evolve in small-bodied organisms like prokaryotes, while senescence and soma evolve in large-bodied organisms like the higher eukaryotes.

Four-fold cost of sexual reproduction

Traditionally it is assumed that sexual reproduction between a male and a female is two-fold costly, but this holds only in a few special cases. More generally, sexual reproduction is four-fold costly because it is both the male individual and the meiotic division of the genome into haploid gametes that are two-fold costly. This does, though, not hold in hermaphrodites that have the potential to bypass the four-fold cost of sex.

Males and sex ratios

According to the classical theory an even sex ratio evolves from sexual reproduction, a diploid or a haplodiploid genome, and random mating (Fisher, 1930). This theory makes sense on a local scale, but it fails on an evolutionary scale where the cost of sexual reproduction implies that

the classical theory is evolutionarily unstable in its assumptions. In consequence, the theory predicts the evolution of asexual variants with no males and no sex ratios.

According to the hypothesis of evolution by density dependent competitive interactions an even sex ratio will evolve in large-bodied mobile organisms independently of the assumptions in the classical theory and despite the four-fold cost of sexual reproduction. Moreover, there is a tendency that relatively small-bodied organisms with low metabolic rates will have female biased sex ratios, while relatively large-bodied organisms with high metabolic rates will have male biased sex ratios. This pattern resembles the general sex ratio pattern among insects, poikilotherm vertebrates, and homoiotherm vertebrates. Finally, if the organism is of negligible size, as is the case in prokaryotes, then the hypothesis of competitive interactions predicts asexual reproduction and the absence of males.

Local mating

According to classical theory local mating is an important factor that induces the evolution of a female biased sex ratio (Hamilton, 1967). This hypothesis makes sense on a local scale, but it fails on an evolutionary scale because the four-fold cost of sexual reproduction selects for a mating pattern that is so local that males do not exist.

According to the hypothesis of evolution by density dependent competitive interactions a female biased sex ratio can evolve independently of local mating and despite of the four-fold cost of sexual reproduction. However, if we assume that sexual reproduction exists and that the genome is diploid or haplodiploid, then the hypothesis of competitive interactions predicts the evolution of local mating when the sex ratio is female biased. In other words, the dependent and the independent variables are changed around, and the new prediction is evolutionarily stable while the old prediction is evolutionarily unstable.

Size dimorphism, male characters, and sexual selection

In many species the size of the male is different from that of the female, and the male has special male characters that can include physiological ornaments or a colourful plumage. According to classical theory these physiological differences between males and females evolve by sexual selection where the females choose the large and the more extravagant males (Darwin, 1859).

According to the hypothesis of selection by density dependent competitive interactions the physiological differences between the two sexes can evolve independently of sexual selection. When this is the case males tend to be larger than females in species with male biased sex ratios, while the reverse is expected when the sex ratio is female biased. This trend is widespread among natural species where birds and mammals tend to have male biased sex ratios and males that are larger than females, while the reverse often is the case in lower organisms, like insects and other invertebrates. Furthermore, the evidence from birds indicates that male characters evolve mainly by competitive interactions, and not by sexual selection. This suggests that female choice and sexual selection evolve from the presence of male characters, and not the other way around, as it has been thought since Darwin introduced the concept of sexual selection.

According to the proposal by Darwin and all subsequent treatments sexual selection is the factor that can explain the physiological differences between females and males from the assumption of sexual reproduction. This is in contrast to the hypothesis of density dependent competitive interactions where sexual selection is the factor that can explain the evolution of sexual reproduction from the physiological and functional differences between male and female individuals. Again, the theoretical results suggest that the dependent and the independent variables need to be changed around.

Sexual reproduction and ploidy level

At least twenty different theories have been proposed to account for the evolution of sexual reproduction. Although these models may explain the evolution of sexual reproduction in hermaphrodites, they fail to explain the general pattern that is associated with sexual reproduction in natural species. This pattern is generally explained by the hypothesis of density dependent competitive interactions, which predicts that sexual reproduction is absent in small-bodied organisms like prokaryotes and viruses, that it exists between males and females in large-bodied mobile organisms, that it exists among hermaphrodites in sessile organisms, and that the optimal solution to sexual reproduction is a diploid or haplodiploid genome with a meiotic division into haploid gametes.

Eusocial colonies

A eusocial colony is characterised by a large worker caste, and eusociality is known mainly from social insects where it occurs in one form in ants and bees, and in another form in termites. These two forms are characterised by two different sets of co-occurring traits: In ants and bees the queen forms the colony on her own after she has mated with a sexual male, the genome is haplodiploid, the workers are the sterile daughters of the queen, and there is typically three queens per sexual male. In termites the queen forms the colony together with the king, the genome is diploid, the workers are the sterile daughters and sons of the queen, and there is typically one king per queen. When we explain the evolution of eusociality it is also essential to explain the evolution of these two patterns of co-occurring traits.

According to classical theory eusocial colonies evolve by kin selection where the sterile workers gain inclusive fitness through the sexual reproduction of their queen (Hamilton, 1964, 1972). According to the hypothesis of selection by density dependent competitive interactions eusocial-like colonies can evolve independently of kin selection when the body mass is upward constrained and there is plenty of resource. This latter result may explain why eusociality is relatively common in insects, where the ecto-skeleton might set an upper limit to the body mass, while it is almost absent in vertebrates, where the body mass seems to be evolutionarily more flexible.

The classical hypothesis makes sense on a local scale, where the workers are assumed to be the offspring of the queen, but it fails on an evolutionary scale where the workers are also allowed be the sexual partners of the queen. In this latter case it follows that it is kin selection and off-spring workers that evolve from the presence of eusocial-like colonies, and not the other way around as originally proposed by Hamilton.

Apart from the transition to eusociality, the classical theory on eusocial colonies is very much restricted to predictions on the sex ratio in the sexuals given the ploidy level of the genome and the sex ratio in the worker caste (Trivers & Hare, 1976). This is in contrast to the theory in Witting (1997) that explains also the evolution of the ploidy level of the genome and the sex ratio in the worker caste given the differences in the mating pattern between termites and ants/bees. Moreover, the causality is generally the opposite in the two theories, where the extended model in Witting (1997) suggests that it is the ploidy level of the genome and the sex ratio in the worker caste that evolve from, or at least are maintained by, a more fundamental selection pressure on the sex ratio in the sexuals, and not the other way around as it traditionally has been thought.

Population dynamics

In the absence of density dependence, the classical theory of population dynamics is based on the Malthusian law of geometrical increase in the population density. This law is based on the assumption that evolutionary changes are absent in the intrinsic growth rate, an assumption

that holds only in the absence of genetic variation. The population dynamic theory in Witting (1997) allows for genetic variation implying that in the absence of density dependence it is based on Fisher's fundamental theorem of natural selection predicting a hyper-geometrical increase in the population density.

Population limitation

Population limitation is the process that determines the equilibrium density, and in the classical theory it is based on the concept that a limiting factor is any factor that, when changed, causes a change in either reproduction, survival, and/or density regulation. This implies that an environmentally induced change in the rate of reproduction and/or survival is converted directly into a change in the population equilibrium. This is in contrast to the population dynamic theory in Witting (1997) where, as a first approximation, the population equilibrium is independent of environmentally induced changes in the rate of reproduction and/or survival.

If the classical theory of population dynamics is combined with the classical theory of selection it predicts that the equilibrium continues to increase until the resource is over-exploited. This is in contrast to observations, and to the hypothesis of selection by density dependent competitive interactions that predicts balanced equilibria where, as a first approximation, the densities at all trophic levels are proportional to the primary production, where poikilotherm vertebrates are approximately 30 times more abundant than homoiotherm vertebrates, where the population density is proportional to the $-3/4$ th power of body mass, and where the exploitation of the resource is body mass invariant.

Population cycles

The population dynamics in natural species tend to be inherently cyclic, and this is unlike the dynamics of the classical theory that is inherently non-cyclic, unless there is some sort of delayed regulation caused by over-compensation or by interactions with other species. It is now generally agreed that over-compensation does not explain the general tendency for cyclic dynamics in natural populations, suggesting that population cycles are caused by predator-prey interactions. However, the predator-prey hypothesis is associated with the paradox that many populations continue to cycle even in the absence of the essential interactions.

According to the hypothesis of selection by density dependent competitive interactions the dynamics of a single species is inherently cyclic, having periods that coincide with the periods in the forest insects with cyclic dynamics. In other words, we no longer have to incorporate interactions with other species in order to explain the cyclic dynamics that occur in natural populations. Moreover, the cyclic dynamics caused by density dependent competitive interactions are associated with a cycle in the intrinsic growth rate, the body mass, and the sex ratio. These latter cycles have been observed in natural populations with cyclic population dynamics.

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