Syst. Zool., 30(1), 1981, pp. 22-31

Structure and Dynamics of Darwinian Evolutionary Theory

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Abstract

A dynamic multi-level model of Darwinian evolutionary theory is presented. Darwinian evolutionary theory consists of interconnected sub-theories and theories at different levels of abstraction. The theory of natural selection is the generic core of the whole structure. Few or no predictions can be directly derived from the generic core. The theory of natural selection generates specific theories and theoretical models which can be empirically tested. Theorizing proceeds through deductive and inductive inferences. The dynamic multi-level model assumes that Darwinian evolutionary theory consists of several competing research programmes and the importance of a pluralistic interpretation of Darwinism is emphasised.

[Evolutionary theory; natural selection; Darwinian; prediction.]

Evolution and natural selection are fundamental concepts in modern biology. However, the predictability and the testability of Darwinian evolutionary theory have been questioned (e.g., Manse., 1965; Peters, 1976; Platnick, 1977; Rosen, 1978). Natural selection has been said to be a logical tautology which explains everything but which is not falsifiable in empirical tests. Consequently, natural selection has been argued to be a dogma, and not a scientific theory.

These arguments assume that the logical structure is the obstacle to testing the theory of natural selection. On the other hand, Williams (1970) and Van Valen (1976) have shown that the theory of natural selection can be presented as a logical deduction. Evolutionary change is a logical implication of the premises presupposed by the theory of natural selection. However, this logical conclusion has little value as a critical prediction for testing the theory of natural selection (Tuomi and Haukioja, 1979a).

Predictability and testability are not merely a question of the formal-logical structure of the theory of natural selection. The other fundamental question is the relations between the theory of natural selection and the other parts of Darwinian evolutionary theory. In order to study this question, the general structure of Darwinian evolutionary theory needs to be analysed and the status of natural selection in this structure specified. Darwinian evolutionary theory is below referred to simply as Darwinian theory.

The Structure of Darwinian Theory

The present analysis is based on two models of the structure of Darwinian theory. The reticulate model is described by Beckner (1968), Ruse (1973), and Caplan (1978). The multi-level model was, presented by Tuomi and Haukioja (1979a).

The reticulate model assumes Darwinian theory to be a complex and flexible structure consisting of interconnected sub-theories. The reticulate model explains why Darwinian theory is so difficult to test (Caplan 1978). Darwinian theory is a logically organized body

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of sub-theories. Not all but some parts of this complex structure can be tested empirically. However, the status of the theory of natural selection is not described in the reticulate model.

The multi-level model assumes Darwinian theory to consist of different levels of abstraction. There are theories which are directly reducible to the empirical level. But, there are also theories which are connected with empirical studies indirectly through theories at lower levels of abstraction. The theory of natural selection is the generic core of this whole theoretical structure. It is a biological meta-theory which has no immediate predictive power. On the other hand, the theory of natural selection is able to generate specific theories and theoretical models which may be predictive and which can be empirically tested.

I propose here a model of Darwinian theory which brings together both the reticulate model and the multi-level model. The model, which I call *the dynamic multi-level model,* describes the structure of Darwinian theory as both reticulate and hierarchical. The theory of natural selection is assumed to be a meta-theory binding the lower-level theories into a hierarchical theoretical structure (Fig. 1A). On the other hand, the lower-level theories can be classified into different sub-theories which form a reticulate structure covered by the meta-theory (Fig. 1B). The model assumes Darwinian theory to consist of four kinds of theories:

1. *The metatheory* (or the generic theory, T_g)

The theory of natural selection shows that evolutionary change is possible through natural selection. In other words, a change in the genetical constitution of populations is a logical implication of the theory. The meta-theory can be presented as a logical deduction (Williams, 1970; Van Valen, 1976) or as a descriptive scheme (Elton, 1927; Mayr, 1977; Tuomi and Haukioja, 1979b). The meta-theory describes natural selection as a process extending from the individual level to the population level. It defines the components of the process and shows their biological relations. But, the general description of the process does not indicate what kind of specific outcomes the process may achieve. The same process is able to generate different kinds of outcomes because the rate and the direction of evolutionary changes depend on the specific conditions at the individual level and at the population level. When changing the specific inputs at these levels, natural selection is able to produce different qualitative and quantitative outcomes, and more specific theories and models of natural selection and evolutionary changes can be generated.

2. *Specific theories* (T_S)

The meta-theoretical description of natural selection is the fundamental abstraction of Darwinian theory. When the fundamental abstraction is enriched with *specific ancillary* (or auxiliary assumptions, s), it is possible to formulate specific theories of evolutionary changes. Specific theories represent different logical possibilities of combining natural selection with other evolutionary factors. The neo-Darwinian genetic theory of natural selection (Fisher, 1930; Wright, 1931; Haldane, 1932; Maynard Smith, 1969) is a specific theory which is formulated by connecting natural selection with Mendelian genetics and random micro-mutations. Alternative specific theories can be generated by introducing other kinds of ancillary assumptions. The theory of natural selection, the meta-theory, presupposes that there exists inheritable variation in populations. However, the meta-theory does not assume any specific mechanism for inheritance (Lewontin, 1970). Specific theories can be formulated by assuming Mendelian inheritance or some other mechanism for inheritance. Variation may be produced by micro-mutations or macro-mutations (Wolsky and Wolsky, 1976). Evolutionary dynamics may also differ in coarse-grained and fine-grained environments (Levins, 1968) or in large and small populations (Kimura, 1979a, 1979b). Specific theories can assume different rules for the operation of natural selection, where selection is assumed to maximize the genetic reproductive success (Williams, 1966; Maynard Smith, 1969, 1978) or to minimize the probability of extinction (Stearns and Crandall, 1980). There also exist several possibilities of defining the unit of selection (Lewontin, 1970) and combining selectionism and neutralism (Gould and Lewontin, 1979). Later in this paper, the theoretical structure, consisting of a specific theory and those theoretical models descending from that specific theory, is called a *research programme* (See also Lakatos, 1970; Popper, 1974).

3. *Theoretical models* (M)

Theoretical models are derived from the specific theories by introducing new ancillary assumptions. Theoretical models are simulations of hypothetical evolutionary changes. Theoretical models generate predictions and test logically the consequences of alternative specific theories. The models define what kind of outcomes are produced by the specific kinds of variations, the specific rules of inheritance, and/or by the specific environmental conditions. In principle, these theoretical simulations are (or, at least, should be) repeatable at the empirical level. The models state that a specific kind of change takes place when the specific conditions (of variation, inheritance, and/or environment) presupposed by the models prevail at the empirical level. These statements are the predictions or the test implications of the models. The predicted kind of outcome should also be the result in laboratory experiments and in natural populations when the empirical conditions satisfy the theoretical conditions presupposed by the models. Williams (1973) and Ferguson (1976) have given several examples of falsifiable predictions derived from theoretical models of natural selection.

4. *Sub-theories* (ST)

The theory of natural selection, the meta-theory, covers almost the whole domain of modem biology (Tuomi and Haukioja, 1979a). Evolutionary biology as a whole is divided into different sub-domains or branches, from systematics and paleontology to population genetics and evolutionary ecology. Each branch emphasises the specific problems of that part of biological reality which is the primary object of study. That is why different branches of biology can also emphasise different aspects of natural selection, depending on what aspects of the whole process are the interest of the study. The division of biology into different branches results in the division of Darwinian theory into different sub-theories. A sub-theory covers one or several domains of biological reality and summarizes those specific theories and theoretical models concerning these domains. The meta-theory of natural selection is the synthesis of the whole Darwinian theory. The sub-theories are more restricted syntheses of those theories presented within a specific domain of Darwinian theory. Ruse (1973) has described a reticulate structure binding together several branches of evolutionary biology. Levins (1968) has shown a more specific description of relations between theoretical components of evolutionary population biology.

The dynamic multi-level model assumes that theorizing in evolutionary biology proceeds through deductive inferences and through inductively introduced statements. Several theoretical steps are needed before the theory of natural selection can be reduced to the empirical level. The number of theoretical levels can vary in different sub-domains of evolutionary biology. In general, however, theorizing follows the same procedure from systematics to population genetics and evolutionary ecology.

As Colless (1969) has pointed out the statement of evolution by natural selection implies that certain unknown phylogenies are true. This statement is not sufficient to predict that two particular species have had the same ancestor. Specific phylogenies can be constructed only when. the meta-theory is logically linked with specific information about interspecific similarity of species and with other empirical information.

The same is true in population genetics, where the rate of change in gene frequencies varies depending on selection coefficients, modes of inheritance, breeding patterns, and other specific conditions (Crow and Kimura, 1970). Predictions are derived in population genetics from theoretical models and not directly from the theory of natural selection. The logical structure of population genetic theory is very complex because frequently a specific mathematical model generates several more specific models. The hierarchical structure consists then of several generations of theoretical models. Levins (1968) also has assumed that theorizing in evolutionary biology consists of different levels of abstraction, and he has specified the theoretical steps of strategic analysis.

In evolutionary ecology ancillary assumptions specify the ecological relations between organisms and their environment. Rhoades (1977), for example, has pointed out that the hypotheses of co-evolutionary processes between plants and their herbivores were not actually generated by a direct deduction from the theory of natural selection. A lot of empirical information was needed before these hypotheses could be formulated. The theoretical models of life-history theory exemplify how the outcome of selection of reproductive tactics can vary depending on specific demographic environments (Stearns, 1976, 1977).

The theory of natural selection, the meta-theory, *per* se does not predict nor explain any specific evolutionary phenomena. A short neck and a long neck are, logically, both equal a priori possibilities for giraffes, and the meta-theory is unable to predict which of these possibilities is more likely to be realized in natural populations (for discussion, see Platnick, 1977). Unless this fact is recognized and if specific evolutionary phenomena are explained directly by the meta-theory without introducing ancillary assumptions, untestable tautologies are the result (Tuomi and Haukioja, 1979a). Tautological reasoning is avoided when testable ancillary assumptions are introduced. Theorizing leads to ad hoc-hypotheses when ancillary assumptions are not tested. The predictive power of Darwinian theory rests on the empirical content of the ancillary assumptions and on the theoretical models combining the logic of the meta-theory with these specific assumptions. Moreover, although the meta-theory *per se is* unable to predict and although it is untestable in a direct empirical test, it is a necessary and fundamental component of Darwinian theory because without the logic of the meta-theory no predictive theoretical models can be formulated.

The Dynamics of Darwinian Theory

The dynamic multi-level model assumes that in Darwinian theory there exist several competing specific theories of evolutionary change covered by the same meta-theoretical frame, the theory of natural selection. Darwinian theory has also experienced major and minor changes in both structure and content. For simplicity I have divided the development of Darwinian theory into different phases. The five phases are described separately, although they may temporarily overlap.

The first phase is the formulation of the meta-theoretical abstraction as a synthesis of empirical observations and theoretical ideas. The *second* phase is the extension of the logical implications of the meta-theory to lower theoretical levels by formulating specific theories and by introducing ancillary assumptions. During the second phase Darwinian theory can be divided into different research programmes which assume natural selection to have a different role as an evolutionary factor. The role assumed by a research programme depends on the specific ancillary assumptions presupposed by the corresponding specific theory. Depending on the ancillary assumptions, specific theories can generate different theoretical and empirical implications although they are logically based on the same meta-theoretical frame.

Darwin formulated the general description of natural selection. But he also made specific assumptions about the origin of inheritable variations. Darwin also assumed that evolutionary changes were produced by small continuous variations which were able to accumulate in populations through natural selection. On the other hand, Galton and Huxley assumed that evolutionary changes take place through the accumulation of discontinuous variations, "sports," by natural selection. In the former case, evolution is a process of smooth and continuous change. In the latter case, evolution is more discontinuous (for details, see Provine, 1971). Darwin's arguments on natural selection were not very exact in details and several interpretations of "Darwinian selection" have been presented. According to Simpson (1953), the original Darwinian concept of selection is that among all the individuals produced in nature some die sooner while others survive longer, and natural selection operates by means of differential mortality. Huxley (1963) has suggested the same interpretation of "Darwinian selection." He stated that this "Darwinian selection" will produce evolutionary changes because the majority of individuals which survive to maturity will leave offspring and because much of the phenotypic variance promoting survival has a genetic basis. According to Driesch (1921) and Waddington (1974) "Darwinian selection" operating by means of differential mortality only eliminates the extreme misfits and does not lead to the selection of the fittest phenotype. Consequently, a part of the inheritable phenotypic variation can be selectively neutral. Kimura (1979a,1979b) has suggested a very similar interpretation of "Darwinian selection." Especially Simpson (1953) and Huxley (1963) have pointed out that the neo-Darwinian interpretation of "Darwinian selection" (e.g., Dobzhansky, 1951) differs fundamentally from the "Darwinian selection" described above. Neo-Darwinian selection is -defined in terms of differential genetic reproductive success without any reference to phenotypic fitness ensuring individual survival (Huxley, 1963). Neo-Darwinian selection results not only in the elimination of the most extreme misfits but selection also drives the population to the optimum which maximizes the genetic output for future generations (Williams, 1966; Stearns, 1977; Maynard Smith, 1978). Neo-Darwinian selection follows Darwin's analogy between artificial selection and natural selection and it is a process in which each genetic variation is incorporated into the population if it has even a slight advantage over the others (Mayr, 1970). These examples show that natural selection can be assumed to operate in different ways. The rules according to which selection operates define the role of natural selection as an evolutionary factor. Even if natural selection is assumed to eliminate only the extreme misfits it would be an essential evolutionary factor, although it would have a more limited role than that assumed by neo-Darwinists (Simpson, 1953).

The *third* phase is the theoretical analysis of the consequences of different specific theories by formulating theoretical models and the empirical evaluation of the theoretical models. During this phase, the interest of the study is in specific evolutionary problems and the meta-theory is of only secondary importance for theorizing. More important is the specific theory and those specific assumptions presupposed by the specific theory and theoretical models. The specific theory performs as the paradigm of a research programme when formulating theoretical models. That is why the idealized hierarchical structure of Darwinian theory described above (Fig. 1A) is not realized as a whole. During the second phase the hierarchical structure extends from the meta-theoretical level to specific theories and during the third phase it extends from the specific theory to theoretical models in each successful research programme.

The early neo-Darwinists showed that Mendelism and Darwinism were complementary. They combined the logic of natural selection with genetic ancillary assumptions and developed quantitative statistical methods for modelling genetic consequences of natural selection (Fisher, 1930; Wright, 1931; Haldane, 1953). Population genetic modelling developed rapidly as the micro-evolutionary research programme (Jepsen et al., 1949; Huxley et al., 1954). In the beginning, the original theory of natural selection was the fundamental theoretical basis for developing specific theories and theoretical models. When population genetic modelling expanded, the importance of the original theory gradually decreased and the specific neo-Darwinian arguments became more important for theorizing. Finally the neo-Darwinian principles were generalized from population genetic models as the paradigm of the micro-evolutionary programme (Maynard Smith, 1969). When the neo-Darwinian paradigm was generalized as the paradigm of evolutionary research as a whole, the meta-theoretical abstraction of natural selection was thrust aside by a more specific abstraction which focussed only on the statistical part of natural selection (Grene, 1961; Tuomi and Haukioja, 1979b). The other part of the process, i.e., the individual level including the relations between organisms and their environment, is assumed implicitly but it is not formulated explicitly. Neo-Darwinists define natural selection as "the differential perpetuation of genotypes" but Mayr (1970) has pointed out that natural selection favours genes or genotypes only indirectly through individuals. Where this fact is not recognized, the role of interactions between organisms and environment is easily neglected in the selection process. When the organism-environment relation is omitted, this does not hurt the logic of population genetic models which analyse the consequences of selection pressures on gene frequencies. However, severe difficulties may result in other branches of evolutionary biology, as in evolutionary ecology where the organism-environment relation is an essential part of causal explanations (Hull, 1974; Tuomi and Haukioja, 1979b). The dynamic multi-level model largely removes this danger, because it interprets neo-Darwinism as a specific research branch of Darwinism, and hence the neo-Darwinian principles cannot displace the general description of natural selection as a meta-theory of the whole Darwinian theory. Branches of evolutionary research other than neo-Darwinism can be equal components of Darwinian theory if empirical studies have not refuted their arguments.

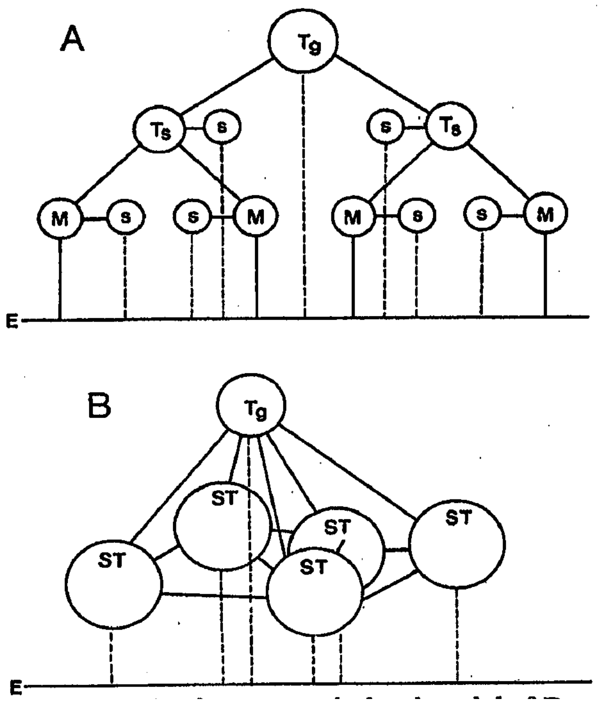

FIG. 1. The dynamic multi-level model of Darwinian theory. The hierarchical structure (A) and the reticulate structure (B) are shown separately. The solid lines represent deductive inferences and the dotted lines represent more or less inductive inferences. T_g = the meta-theory, T_s= a specific theory, M = a theoretical model, s = specific ancillary assumptions, ST = a sub-theory, and E = the empirical level.

The *fourth* phase is the formulation of syntheses within different research programmes and within different domains of evolutionary biology. During the second phase and third phase, the structure of Darwinian theory is primarily hierarchical. Now the structure becomes more reticulate (Fig. 1B). In the micro-evolutionary programme, the theoretical analyses were supplemented by laboratory experiments (Dobzhansky, 1951) and later by ecological genetics (Ford, 1964). Simpson (1953) also applied population genetic principles to macro-evolutionary phenomena. The micro-evolutionary programme expanded into different branches of biological sciences and gradually the theoretical structure was divided into different domains and sub-theories (Caplan, 1978). The synthetic theory (e.g., Huxley, 1963; Mayr, 1970) was formulated as a summary of the most important theoretical and empirical results produced by the micro-evolutionary programme.

The fifth phase is the comparison of the intra-paradigmatic sub-syntheses of different research programmes. The result of the comparison may be a general synthesis of Darwinian theory which may cause a revision of the meta-theoretical abstraction leading to a revision of the lower theoretical levels. The most important point is that the synthetic theory is primarily an intra-paradigmatic sub-synthesis of the neo-Darwinian micro-evolutionary programme. Other alternative research programmes are only superficially represented in the synthetic theory (Stearns, 1979). At the present moment more general syntheses are needed (for discussion, see Wolsky and Wolsky, 1976).

The peculiar character of the dynamic multi-level model is that Darwinian theory is assumed to be an inconsistent body of specific theories and theoretical models. The contradictions between specific-theories, between theoretical models, and between theoretical models and empirical data constitute the sources of dynamic changes in Darwinian theory. Changes can take place at every theoretical level, including the meta-theoretical level. The testing of Darwinian theory includes both empirical analysis and theoretical analysis of the theory. It includes empirical tests of theoretical models, theoretical analyses of the consequences of specific theories, and theoretical analyses of the contradictions between specific theories. Darwinian theory does not provide (or should not provide) only one explanation of evolution but several explanations. Since the causes of evolutionary changes vary in time and in space, there cannot be a specific theory to explain every specific evolutionary change. Each specific theory is a logical possibility which can be true in one or several domains of biological reality.

Now the fundamental scientific value of the meta-theoretical level can be fully recognized. This level permits the synthesis of different logical possibilities and an objective theoretical and empirical analysis of these possibilities. (By the term "objective" I mean the situation in which the person has no subjective beliefs in the truth of any specific theory.) If there is no such meta-theoretical level or if the meta-theoretical level is assumed only implicitly, Darwinian theory breaks down into contradictory research programmes. Then each programme provides a consistent picture of a part of the whole process but the whole picture of evolutionary phenomena has collapsed. Consequently, there is a danger of subjectivism and dogmatism. Scientists defend their own programmes without recognizing that each programme provides only a partial explanation of evolutionary phenomena. The truth is not one of these alternatives but an unknown combination of them.

Discussion

The most important advantage of the dynamic multilevel model is its comprehensive approach to evolutionary biology. It can serve as a useful basis when synthesising different evolutionary ideas and theories into the same theoretical structure. When the theory of natural selection is interpreted as a meta-theory, it does not include any specific assumptions about variation, inheritance, environment, and other specific problems.

Both the neo-Darwinian genetic theory of natural selection and the neutral theory of evolution are specific theories which assume natural selection to be an essential evolutionary factor. When Mendelian genetics was rediscovered, it provided an available pool of ancillary assumptions for the early neo-Darwinists. Then it was possible to analyse theoretically the genetic consequences of natural selection. However, not only Mendelian inheritance but also non-Mendelian inheritance can provide useful ancillary assumptions for theorizing in evolutionary biology. Waddington (1957) and Reidl (1977), in particular, have emphasised the fundamental role of physiological and developmental biology in evolutionary phenomena. Genetic processes are an essential part of natural selection. But ecological relations between individuals and their environment are also an essential part of natural selection (Slobodkin and Rapoport, 1974). It is these relations that determine which individuals survive or are eliminated from populations, and natural selection loses much of its empirical content if the ecological interactions are omitted (Hull, 1974; Brady, 1979).

According to Kuhn (1962) science develops through normal science and periodic scientific revolutions. Normal science emphasises dogmatism and intra-paradigmatic consistency. Science drifts into a crisis when there exist two or more competing paradigms. As a result of the crisis the old paradigm may be displaced by a new paradigm. After this scientific revolution there is again a long period of normal science. The process of the dynamic multi-level model is Kuhnian in the sense that the theory of natural selection is the universal paradigm of Darwinian theory and each specific research programme develops through normal science. Although the , lower-level theories must be logically consistent with the theory of natural selection, there can be contradictions between specific theories and between specific research programmes. Because Darwinian theory includes several specific research programmes the whole theoretical structure is in a permanent state of Kuhnian crisis or in a permanent state of competition between specific theories and between research programmes. Husserl's (1962) concept of scientific crisis differs fundamentally from the Kuhnian concept of Brisis. When science as a whole is characterized by normal science, this is, according to Husserl, a reflection of a crisis in which the scientific community has lost its objectivity and is no longer aware of its theoretical and empirical context.

This kind of crisis is the result in Darwinian theory when the meta-theoretical status of the theory of natural selection is not recognized. Consequently, the meta-theoretical abstraction is replaced by a more specific paradigm and competition between research programmes is relaxed by eliminating the other, alternative specific theories from the whole theoretical structure. The question of the predictability and the testability of natural selection would seem to reflect a crisis in which the theoretical and empirical context of natural selection is not universally recognized.

The theory of natural selection is not a logical tautology. However, few or no predictions can be directly derived from the theory of natural selection. The theory of natural selection is indirectly connected with the empirical level when specific theories and theoretical models of natural selection are generated by introducing ancillary assumptions. Originally the theory of natural selection provided naturalists with understanding and potential possibilities for explanation and prediction. Later, natural selection was logically combined with explanations of biological adaptation which have been recently criticised (Ghiselin, 1966; Lewontin, 1972; Brady, 1979; Gould and Lewontin, 1979). Neo-Darwinists succeeded in giving a more predictive content to the logic of the theory of natural selection, although their mathematically sophisticated models are sometimes very difficult to test (Lewontin, 1974; Rosen, 1978).

The interpretation of the theory of natural selection as a biological meta-theory is not an entirely unique phenomenon in the natural sciences. Bunge (1973) has given examples of meta-theories in the physical sciences. Also systems theory, which is generally used in the biological sciences, is a meta-theory (Blauberg et al., 1977). Meta-theories seem to be most valuable in science although they are not testable in direct empirical tests. Their functional dimension in science is not prediction nor explanation, but rather understanding (von Wright, 1971). The meta-theory gives a rough picture of the whole problem by logically combining fundamental definitions and concepts. Specific theories and theoretical models describe sub-problems in detail by means of explanation and prediction.

Acknowledgments

Arthur Caplan attracted my attention to the relatedness of the reticulate model and the multi-level model. I also wish to thank Tuomo Hakala, Erkki Haukioja, Ossi Lindqvist, Stephen C. Stearns, and Paavo Voipio for critical comments, and Miss Terttu Laurikainen for drawing the figures. The work was supported by the Academy of Finland.

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Philosophy of Science, 59 (1992) pp. 429-438.

Evolutionary Synthesis: A Search for the Strategy

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The goal of evolutionary theory is to (a) specify the general causal structure of evolving systems and (b) analyze evolutionary consequences that are expected to result from the proposed structure of the model systems. Biologists frequently emphasize the hypothetico-deductive method in evolutionary theory. I will show that this method primarily provides a tactical device for (b), while evolutionary synthesis requires a foundation of a unifying conceptual model for (a). Therefore, any successful strategy for a new synthesis requires both a new conceptual insight of evolving systems, and tactical devices for analyzing new specific aspects of the evolutionary process.

1. Deductive Structure in Evolutionary Biology

Ghiselin (1969) proposed that the hypothetico-deductive method provided the basic methodological strategy of the *Origin of Species* ([1872] 1962). Indeed, the basic theoretical elements of Darwin's theory can be arranged into a set of deductive arguments (Williams 1970, Ruse 1971, Van Valen 1976, Lewis 1980). However, this method is not able to bring the arguments into a single axiomatized deductive system (Ruse 1975, Recker 1987, Sintonen 1990).

A reason for this may be that evolutionary theory represents a complex network of sub-theories concerning, for example, adaptation, microevolution, speciation, and macroevolution. I have argued earlier (Tuomi and Haukioja 1979, Tuomi 1981) that this theoretical structure is organized by two major theories (sensu Lewis 1980), the theory of descent with modification and the theory of natural selection. These major theories created the basic conceptual framework of the *Origin of Species,* which was indirectly related to specific questions and theories in terms of various auxiliary hypotheses (see also Lewis 1980, Bradie and Gromko 1981, Wassermann 1981, Burian 1988, Mayr 1988).

The auxiliary hypotheses must be separately invented in each specific case. This leads to a succession of theories from the given major theory (T_0). .

(i) T_0: $H_0 \supset P_0$

towards more specific theories

(ii) H_0 & H_I

(iii) H_0 & H_I & H_{IJ}

where H_0 specifies the basic properties of evolving systems, P_0 denotes the fact of evolution as implied by H_0, H_I is a set of auxiliary assumptions for a domain (I) of problem solving, and H_{IJ} indicates further auxiliary assumptions that are proposed for resolving given problems (J) within this domain. This explains several basic features of evolutionary theory. First, the theory is characterized by a temporal succession of theories (e.g., Lakatos 1970). Second, it has a hierarchical structure where the abstract major theory (T_o) is gradually enriched with specific hypotheses, H_I and H_{IJ}, and data (Bunge 1978). Third, the hierarchical structure can branch out towards various domains of problem solving if appropriate auxiliary hypotheses, say H_I and H_J are invented (Tuomi and Haukioja 1979). Fourth, alternative specific theories can be generated if competitive auxiliary assumptions are introduced, for example, H_I versus H'_I or H_{IJ} versus H'_{IJ} (Lewis 1980, Tuomi 1981).

Fifth, a reticulate structure of the theory-net results if different specific theories share partially same premises (Caplan 1978, Tuomi 1981).

This sketch of the structure of evolutionary theory may be largely consistent with the more rigorous semantic and structuralist views of scientific theories (for a lucid discussion and references, see Sintonen 1990). It seems to me, however, that the semantic model concept alone, which is a set-theoretical entity (a specific interpretation which satisfies the premises of the abstract theory), may be insufficient to highlight the basic functions of biological theories. Instead, biological theories are more closely related to the ordinary model concept (e.g., Bunge 1973, Nurmi 1975) insofar as their goal is to represent the structure and function of biological systems. They either specify theoretical model systems or present hypothetico-deductive arguments concerning the behavior of the model systems.

This leads to my present argument that the goal of evolutionary theory is to (a) specify the general causal structure of evolving systems and (b) analyze evolutionary consequences that are expected to result from the proposed structure of the model system. The major unifying theories (T_0) present the most fundamental and general properties of evolving biological systems, and more specific theories are generated in terms of H_I and H_{IJ}, that introduce specific causal elements and relations. Deduction is used to prove that the proposed causal structure can lead to evolutionary change (i), or to derive more specific predictions

(iv) $H_0 \& H_I \& H_{IJ} \supset P_{IJ}$

where P_{IJ} states the expected behaviour of the system under a given set of specific assumptions. If so, then the hypothetico-deductive method is mainly related to these analytical steps of the theory.

2. Conceptual Models of Evolving Systems

The above discussion suggests that the basic unifying theories in evolutionary biology are likely to represent conceptual models of evolving systems rather than predictive or explanatory laws (Tuomi 1981; Mayr 1982, 1988). For this purpose, I will show below how the major revolutions in evolutionary thinking, from Lamarck to the modem synthesis, have implied fundamental innovations in the causal structure of evolving systems. I do not try to present any historically accurate description of the development of evolutionary theory. Instead, I demonstrate that each major theory presupposes implicitly or explicitly specific kinds of relations between ontogeny, inheritance and environmental interactions.

2.1 Lamarckian Model

The Lamarckian theory presupposed that phenotypic traits of individual organisms are modified in relation to their adaptive needs. If these acquired characters are also transmitted to descendants, the offspring would be inherently better adapted to their places in the economy of nature.

I consider that this model of adaptation tries to draw an analogy between organismic and cultural evolution. Human artefacts, such as tools for instance, evolve from the first primitive designs. The designs are tested in practice in relation to given functions, and improved to reach higher functional efficiency. Eventually, a variety of designs may thus arise from the original unspecialized model for slightly different specialized tasks and purposes., The key factor in this development is a feedback between design, function and modification. An analogous feedback is also proposed by the Lamarckian model of adaptation (figure 1).

This feedback model may be best presented by dividing the adaptation process into three basic components: (a) ontogeny modifying the phenotypic features of individual organisms, (b) functional relations between the phenotypic features and given environmental conditions, and (c) transmission of phenotypic variations from one generation to the next. A feedback loop can thus be created if (i) ontogeny influences phenotypic traits, (ii) phenotypic traits influence functional interactions, and finally (iii) functional interactions influence ontogenetic development (see figure 1). This feedback system could thus, at least in theory, modify phenotypic traits of organisms in relation to their functional needs, whereas transmission merely maintains the persistence of the adaptive changes.

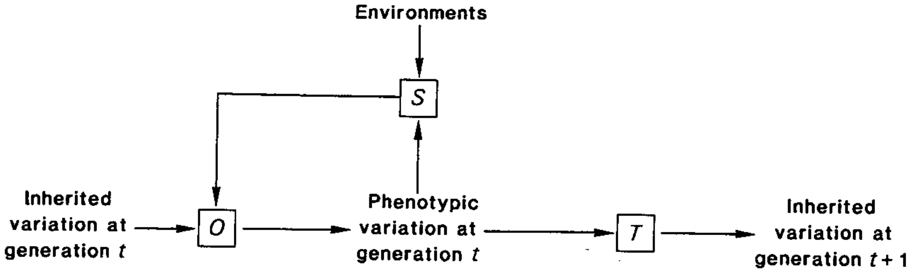

Figure 1. A Lamarckian model of adaptation involving a feedback between ontogeny (O) and functional interactions (S). Due to the feedback loop phenotypes are modified for the adaptive requirements of organisms, and such acquired phenotypic variation is transmitted (T) to the succeeding generations.

The feedback model provides a possible model system which satisfies the basic tenets of the Lamarckian theory. The main function of the model is that it tells us how ontogeny, functional interaction and inheritance should be related if the theory is true. If the real systems also had this same causal structure, we could expect that they can evolve by means of the inheritance of acquired characters. If not, we should reject the theory as a plausible explanation of adaptation. Consequently, for disproving the theory, we may carry out experiments in order to show that acquired characters are not inherited by the offspring, or alternatively we may attempt to prove that the causal structure of the actual systems does not satisfy the presuppositions of the theory (for an example, see Maynard Smith 1989).

The Lamarckian model of adaptation is important at least in two ways. First, it includes some causal elements which were also incorporated into the Darwinian model of natural selection. Second, although it evidently has been unsuccessful in explaining genetic evolutionary changes, it may still be useful in modelling some aspects of cultural evolution.

2.2 Darwinian Model

We need, in fact, only minor structural changes in the Lamarckian model (figure 1) to generate Darwin's theory (figure 2). Surprisingly, population thinking as such (e.g., Ghiselin .1969; Mayr 1982, 1988) has no extensive impact on the causal structure of the model. What seems to be more fundamental is organism-environment interaction since "the conditions of life may be said, not only to cause variability, either directly or indirectly, but likewise to include natural selection, for the conditions determine whether this or that variety shall survive" (Darwin [1872] 1962, 140).

As frequently emphasized, Darwin did not reject the inheritance of acquired characters. His environmentally induced variability (figure 2) did not, however, imply such a feedback loop as did the Lamarckian model (figure 1). Instead, the designs of adaptations were gradually molded by selection operating through successive generations. At each generation the various phenotypic features of individual organisms contribute to their ecological interactions with the environment, and these interactions in turn determine the success in survival and in leaving progeny (Tuomi and Haukioja 1979). In this sense, these interactions can be said to comprise a phenotypic selection process (S_P, figure 2) that modifies the survival and reproduction of organisms as a function of their phenotypic features.

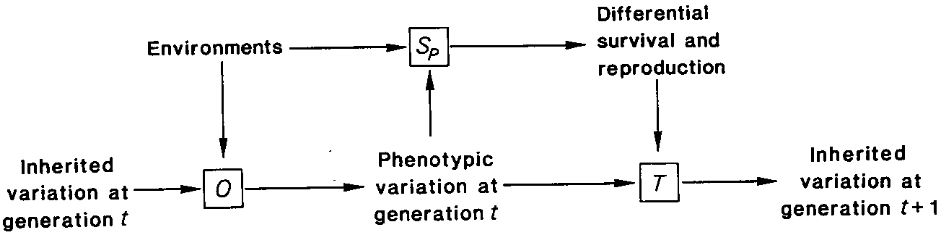

Figure 2. Darwin's model of adaptation-involving phenotype-environment interactions (S_P) which modify survival and reproductive success of organisms. This phenotypic selection process affects the rates at which inheritable traits are propagated (T) to the succeeding generations. The environment may also influence ontogeny (O) and the consequent phenotypic modifications may, at least partially, be transmitted to offspring.

The struggle for existence was just a metaphorical way to propose a specific hypothesis for the operation of phenotypic selection. If we assume that the functionally superior (best adapted) individuals enjoy higher reproductive fitness and that their properties are inheritable, these "best adapted individuals ... will tend to propagate their kind in larger numbers than the less well adapted" (Darwin [1872] 1962, 97). I thus consider that this principle of natural selection together with the premises outlining the causal components of the selection process (figure 2) comprised the original theory of natural selection. If the actual evolving systems had such a causal structure that the theory requires, and if functionally superior individuals will really enjoy selective advantage due to their inheritable characters, we could expect the systems to be capable of evolving by means of natural selection as the principle postulates.

Adaptation by natural selection, or shortly Darwinian evolution, involves gradual inheritable changes in populations. If the selection process operates through successive generations according to the principle of natural selection, favourable inheritable variations should accumulate in populations, while injurious variations are gradually eliminated by selection. Functionally neutral variation which affects neither survival nor reproduction may remain either as "a fluctuating element" in populations or become fixed due to factors other than selection (Darwin [1872] 1962, 91). This is in a surprisingly good agreement with the present views that the fixation of adaptively neutral mutations is a more or less random process, whereas selection is the basic evolutionary force molding adaptive features of organisms.

These scenarios of Darwinian evolution represent deductive arguments which analyze hypothetical evolutionary consequences that can be expected to result in the model system under specific conditions. The arguments demonstrate that the model system works: It is capable of generating a variety of evolutionary changes depending on the specific relations between the basic causal components of the entire process.

Evidently, the main goal of the third and fourth chapters of the *Origin of Species* was to outline the causal elements and structure of the selection process, and to specify how the process modifies genetic composition of populations, and how such genetic changes may gradually lead to adaptation and speciation. Since Darwin further tried to prove that his basic premises cannot be doubted and that a large number of specific instances are likely to satisfy the requirements of his theory, the *Origin of Species* become eventually a long and messy argument for demonstrating the potential explanatory power of the selection theory (Hodge 1977, Recker 1987, Sintonen 1990).

2.3 Neo-Darwinian Model

Weismann proposed that inheritable variations are transmitted from a generation to another by a substance ("germ plasm") which is located in the nucleus of germ cells and which differed from another substance, "soma". These substances were already distinguished in germ cells and they remained so during the ontogenetic development. Somehow "soma" was not transmitted to decendants; they only inherited "germ plasm" from their :parents. This somewhat metaphysical theory is frequently supposed to imply that the inheritable material is transmitted along the germ line leading from a zygote to new gametes. This would be the case if the germ line is sequestered from somatic cells at an early state of ontogeny. In such cases, neither genetic changes nor purely phenotypic modifications in somatic cells are inheritable (for details, see Buss 1987).

The theory of germ line has several implications for our conceptual image of the adaptation process. Evidently, due to the separation of the germ line and somatic cells, we should delete functional feedbacks (figure 1) between ontogeny and transmission of hereditary material, as well as the inheritance of environmentally induced phenotypic variability (figure 2). In order to keep ontogeny and phenotypic selection conceptually separate from each other, we should also distinguish epigenetic environments related to the former from the ecological organism-environment interactions which are involved in phenotypic selection (Tuomi et al. 1988). When these revisions are made to the original Darwinian model of adaptation (figure 2), we can perceive ontogeny, phenotypic selection, and transmission as conceptually separate but causally interconnected sub-processes (figure 3).

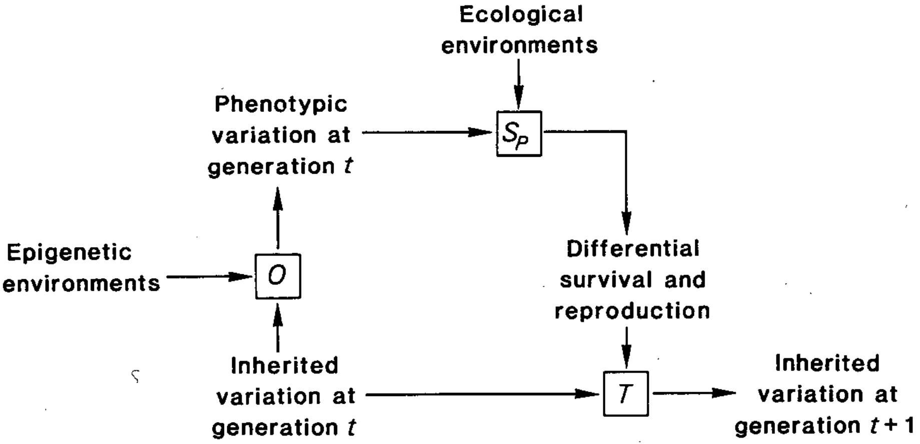

Figure 3. A neo-Darwinian model of adaptation in which developmental modifications are not transmitted to the succeeding generations. Symbols the same as in figure 2.

Consequently, adaptation can be outlined as a process in which (i) hereditary material modifies phenotypic features of organisms, (ii) the traits undergo functional tests in phenotypic selection; and (iii) the consequent fitnesses of their carriers modify the rates at which hereditary material producing these traits are propagated to the succeeding generations. This reasoning represents a basic neo-Darwinian view of Darwinian evolution, that is, genetic adaptation by natural selection. Darwinian evolution can be conceptually distinguished from non-Darwinian evolution which does not involve selection as a causal force of genetic changes, as well as from cultural evolution which is based on cultural transmission associated with epigenetic modification of behavioural features.

2.4 The Modern Synthesis

Population genetics is frequently claimed to be the unifying deductive core of the modem evolutionary theory (e.g., Ruse 1973). This claim is not exactly true, since the population genetics theory merely represents a speciality for analyzing the specific genetic aspects of evolutionary change (Tuomi 1981, Mayr 1988). One cannot, however, deny that theoretical population geneticists (e.g., S. S. Chetverikov, R. A. Fisher, J. B. S. Haldane and S. Wright) had a fundamental impact on the basic conceptual framework of the modem synthesis, as outlined by T. Dobzhansky, J. Huxley, E. Mayr and G. G. Simpson among others. Both groups of evolutionary biologists were affected by the rapid expansion of genetics from the rediscovery of Mendelism to the establishment of the gene theory with the consequence that they developed the neo-Darwinian theory toward a more elaborated genetic theory of evolution.

Although the founders of the modem evolutionary theory did not completely agree with each other concerning the relative significance of various evolutionary forces (e.g., selection and random drift) and they proposed alternative genetic models of evolution (Wright 1980), they consistently formulated evolutionary concepts in population genetic terms (for details, see Tuomi et al. 1988). Consequently, a change of gene frequency was considered as the elementary process of evolution, or more frequently as the evolutionary change itself. Selection was specified in genetic terms as non-random change in gene frequency, non-random differential reproduction of genotypes, or differential propagation of gene alleles and gene complexes. The logic of these black box definitions (sensu Darlington 1983) of selection is most nicely summarized by Lerner (1958, 1959).

Since selection was mainly used as a technical term ("serving to say that some genotypes leave more offspring than others", [Lerner 1958, 10]), the original principle of natural selection could "now be paraphrased to say (1) that in nature individuals differ among themselves, (2) that their differences are in part determined by heredity, and (3) that, therefore, whenever these differences are correlated with fitness, that is, success in leaving offspring, the properties of the more fit individuals will be represented in succeeding generations to an increasing extent" (Lerner 1959, 176; see also Williams 1970). What is so characteristic of this reformulation of the theory is that selection is completely perceived "in terms of its observable consequences" (Lerner 1958, 5), without specifying the ecological interactions which are involved in phenotypic selection (SP, figure 2) and which actually determine correlations between fitness and given phenotypes. An obvious explanation for this is that these phenotype-environment interactions were considered to be irrelevant for analyzing the genetic basis of evolutionary change (Lerner 1958).

The modem synthesis thus above all established a unifying conceptual framework for a genetic theory of evolution,. while the deductive method was primarily used at the sub-theory level, for example, in population genetic models.

3. Conclusions

The hypothetico-deductive method plays without any doubt an important role in evolutionary theory, as. suggested by Ghiselin (1969) and Ruse (1973). However, it mainly provides a tactical device for analyzing and resolving specific questions rather than a strategy for a conceptual synthesis over the entire evolutionary theory.

A reason for this is that the hypothetico-deductive method allows us to take shorter deductive steps for deriving consequences which will follow from a limited number of premises. These deductive steps build up separate theories, that is, single hypothetico--

deductive arguments. The arguments in turn are explicitly, or many times implicitly, anchored to the reality via conceptual models or ideas of the systems that the theories are supposed to deal with. The Lamarckian theory presupposes a causal feedback between functional interactions and ontogeny. Darwin's theory revised this scheme by relating functional interactions with selection. The neo-Darwinian model explicitly deleted the functional feedbacks between ontogeny and transmission of hereditary material. The modem synthesis developed .the neo-Darwinian theory further toward a more rigorous genetic theory of evolution by reformulating the basic concepts (e.g., evolution and selection) in genetic terms.

At this abstract level, the development of evolutionary theory can be seen as a conceptual puzzle in which each major theory tries to build up a general conceptual synthesis over the fundamental properties of evolving systems. All the specific theories which share the same basic causal structure are thus integrated into the same unifying conceptual framework. The integrative power of any basic theory depends on (a) the potential number of specific theories that the theory is able to generate, and (b) the explanatory and predictive content that the subordinate theories will actually have in relation to specific aspects of evolution and adaptation.

This vision of evolutionary theory implies that we need both a unifying conceptual model of evolving systems and technical devices for more detailed evolutionary analyses in order to create successful evolutionary syntheses. Darwin's theory may provide important clues for such attempts. Darwin created a unifying conceptual framework by connecting developmental processes, transmission of hereditary, material and ecological organism-environment interactions into a single evolving system. His success, however, largely relied on his principle of natural selection which provided him and his followers with a powerful logical device for generating specific hypothetico-deductive theories of evolution and adaptation. We need such principles for analyzing adaptation by natural selection while the principles as such may tell us relatively little about the causal structure of the selection process as a whole.

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