

THINKING ABOUT MODELS IN EVOLUTIONARY THEORY

Elisabeth A. Lloyd

Scientific theories present descriptions of abstract or ideal systems, according to the semantic view of theories. These ideal system descriptions — commonly called “models” — are used to explain systems in the natural world. On the semantic view of theories, scientific explanations have several components: descriptions of the ideal system; the hypothesis that a system in the natural world is isomorphic to or matches the ideal system in some significant aspects; and the specification of the range or scope of natural systems which are to be explained using the model. I believe that the picture presented by the semantic view of the nature and form of empirical claims can help clarify some important disputes in evolutionary theory; empirical evaluation of competing claims presumes agreement and understanding of the exact nature of those claims. I suggest that the semantic approach to theories offers a useful framework for sorting out the exact nature of competing claims within several widely-debated areas of evolutionary theory (for a detailed presentation of the semantic view, see Suppes 1957, 1967, van Fraassen 1970, 1972, 1980, and Suppes 1972, 1977; for application of the semantic approach to evolutionary theory, see Beatty 1980, 1981, 1982, Thompson 1983, 1985 and Lloyd 1983, 1984).

1. Models, empirical claims, and ranges of application

Scientists present descriptions of ideal systems. These can be specified mathematically or informally, at various levels of abstraction. Models can be more or less abstract, depending on what proportion of the parameters and variable values is specified. For instance, a population genetics model can be defined that includes a migration parameter, but in which the value of that parameter is unassigned. An identical model in which the migration parameter

is specified is less abstract than one in which it is not.

Informal models can also be specified at various levels of abstraction. For example, natural selection models can be defined which assume the existence of *some* environmental pressure that reduces the population in question. More specific models could describe the exact nature of that environmental pressure, e.g., competition for food, or the existence of extreme weather conditions (see Lloyd, 1983, for an extended discussion of informal selection models and evolutionary explanations; see also Kitcher, 1985). These more specific models would, presumably, be used by evolutionists to explain a narrower set of natural systems; however, the range of application is not specified when the ideal system itself is defined. The scientist simply describes how a system works in the abstract — its components and measures, and their interactions and interrelations.

Ron Giere has called the application of a model to a natural system the “theoretical hypothesis” — I think “empirical hypothesis” might be more appropriate, since it is only at this point in scientific practice that any empirical claim is being made. Giere claims that theoretical hypotheses have the following general form : “The designated real system is *similar* to the proposed model in specified *respects* and to specified *degrees*.”

One problem with describing empirical claims in this fashion is that *general* empirical claims are not visible. While we can understand general claims to be aggregates of specific claims, there are also cases in which debates in evolutionary theory revolve around the *range* of applications of a specific model or model-type; these are more general, higher level (but still *empirical*) claims than the paradigmatic “matching” claim usually described by semantic view theorists.

I suggest that thinking about some of these higher level, more general claims in evolutionary biology can be aided by a precise understanding of the nature of the models and how they might be applied. The debates about selectionism and about group selection vs. individual selection are, for instance, often described as “theoretical” debates. I suggest that this name is a bit misleading — buried in the conceptual confusions and fuzzy definitions are *empirical* disputes.

Take a simple population genetics model, e.g., the Hardy-Weinberg equilibrium. There is a wide variety of empirical claims that could be made using this model.

A biologist could choose a single natural population, say, of

ants, and make the empirical claim, "this ant population is described ("best described," "modeled by," "isomorphic in some respects to") a Hardy-Weinberg equilibrium model. This is the simple sort of instance of matching usually described by semantic view theorists. The biologist could also make a different sort of empirical claim: "all ant populations are described by Hardy-Weinberg equilibrium models," or even, "all populations of all organisms are described by Hardy-Weinberg equilibrium models." These latter claims differ in scope or range from the first. Obviously, the latter claims are higher level claims, encompassing numerous instances of the specific claim regarding the single ant population.

Any empirical claim, then, involves an explicit or implicit assumption regarding the *range of applicability* of the ideal system described by the theory. In fact, some empirical claims can be best understood, not as claims that some particular system is best described by a model, but that a specified collection of systems *each* can be described by the *same* model, or, more specifically, by the same model-type. I think that some "theoretical" debates in evolutionary biology are best understood primarily as empirical debates regarding the range of applicability of a particular model or model-type. Hence, I expect that clarification of these empirical claims and their relation to differences in theory will benefit the conceptual and theoretical debates, particularly those concerning adaptationism, group selection, and macroevolution.

2. Selectionist Debates

One of the primary questions in the selectionist/adaptionist debates concerns the range of applicability of selection models; that is, can *all* populations at all times be described accurately by selection models? (A related but distinct issue is: should all biologists look for selection model applications at all times?) For the purposes of this discussion, all types of selection models are included under this rubric — gene selection, group selection, sexual selection, etc.

I would like to reformulate the above selectionist question in terms of competition between types of models. In theory, a number of different models could be given to account for specific traits of a population or species, including genetic drift, genetic hitchhiking, developmental channeling, etc. The question is, which of these possible models best describes a given particular system in nature?

Furthermore, are selection models so often superior in the accuracy of their descriptions that no other models need be considered?

Biologists R.C. Lewontin and S.J. Gould comment about the consideration given to alternate models among practising biologists.

“We wish to question a deeply engrained habit of thinking among students of evolution... the near omnipotence of natural selection on forging organic design and fashioning the best among possible worlds. This programme regards natural selection as so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function, and behaviour. Constraints upon the pervasive power of natural selection are recognized of course... but they are usually dismissed as unimportant or else, and more frustratingly, simply acknowledged and then not taken to heart and invoked.” (Gould and Lewontin 1979, pp. 584–585).

They continue :

“At this point, some evolutionists will protest that we are caricaturing their view of adaptation. After all, do they not admit genetic drift, allometry, and a variety of reasons for non-adaptive evolution? They do, to be sure, but we make a different point. In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival, but *circumscribe its domain of action* so narrowly that it cannot have any importance in the affairs of nature... We maintain that alternatives to selection for best overall design have generally been relegated to unimportance by this mode of argument.” (Gould and Lewontin, 1979, p. 585, my emphasis).

Note that the debate centers around the range of applicability of the various types of competing models, including selection models. Gould and Lewontin’s complaint is that the alternative models are not seriously considered in the daily practice of the biologists (see Gould and Lewontin, 1979, p. 586). John Beatty has offered an insightful analysis of why such practice might be considered objectionable.

Beatty has described the selectionist debate as a discussion regarding the division of scientific resources. Biologists can spend their time pursuing (formulating and testing) natural selection hypotheses, drift hypotheses, or both. (We shall limit ourselves, in the rest of this discussion, to consideration of the two leading competing models, selection and drift.) Beatty argues that, while selectionists do pursue particular selection hypotheses, this does not mean that they have necessarily made up their minds about the truth of the particular hypothesis, nor about the general evolutionary importance of natural selection.

Beatty characterizes Gould and Lewontin's critique of panselectionism (Gould and Lewontin, 1979) as a complaint that too many biologists are pursuing selection hypotheses; he disagrees with the commonly held interpretation that Gould and Lewontin think that too many biologists accept that selection is an all important force in evolution. (See Dennett, 1983, and commentators for a variety of interpretations of Gould's and Lewontin's views.) Gould and Lewontin think it is unreasonable, Beatty asserts, for the community of biologists to have almost all of the available resources pursuing selection hypotheses, since this is not the most effective way to tell whether selection is or is not the prime force in evolutionary change.

Beatty argues that alternatives for specific systems will not even be *considered* unless the general question about the role of selection in evolutionary change as a whole is being taken seriously. That is, if questions about the overall importance of selection vs. drift are being asked, then it becomes necessary to consider alternatives for particular cases. Only in this way can information be compiled to answer the more general question.

Beatty's interpretation supports the view that the selectionist debate concerns which type of models — selection, drift, combined drift/selection, or other types of models — has a broader or more significant range of applicability. Gould and Lewontin's concern, I think, is that biologists are not merely making guesses about which models will be more widely applicable, but they are also neglecting to collect evidence that could help determine the comparative applicability of the various types of models.

Defenders of adaptationist approaches reply that the search for selectionist explanations of the presence of traits is the only possible strategy for the practising biologist (Mayr 1983). Under this view, a biologist should appeal to drift (or to developmental constraints)

only as a last resort. It is precisely this unwillingness to consider alternative models that undermines the effort to determine the adequacy of selection models in general.

Elliott Sober has recently reformulated the selectionist question in terms of forces; he asks what it means to say that natural selection is the overwhelmingly most powerful force of evolution. The theoretical problem then becomes: how are we to compare the relative force of various component forces of evolution? (Sober, paper delivered 1985).

Using the standard population genetics model, Sober begins with a comparison of a selection model vs. a selection and mutation model. Sober then compares selection and drift as components of evolution, and argues that this case is fundamentally different from the selection vs. mutation case.

The tools of the semantic view enable these distinctions to be made in a precise, economical way. It is possible to compare directly the "force" of mutation and the "force" of selection because both mutation and selection can appear as parameters in a model which is couched in terms of genotype frequencies. It is not possible, however, to compare directly the force of selection and the force of drift in a given model; the two processes are usually represented by models with different types of state spaces. That is, selection models are customarily presented in terms of genotype frequencies, while drift models are couched in terms of a probability distribution of genotype frequencies.

Thus, the two types of model, selection and drift, should be understood as competing models. They are clearly not competing models for any single system; rather, they are alternative models for aggregates of systems. When considering the range of application of a type of model, then, one attempts to apply the model to a set of natural systems — the empirical evaluation involves matching of the model's frequency distribution with that measure from the natural systems. Consider models which present both selection and drift. Selection is taken to operate directionally; that is, it influences the frequency distribution of gene frequencies in the collection of populations in a non-random way. Hence, the collection of populations is expected to have different characteristics under selection and drift models and drift models alone. The point, again, is to evaluate empirically which type of model best describes the ensemble of populations.

A variety of issues appears in selectionist debates... only some

really involve the question of how powerful selection is compared with other causes of evolution. Sober says it is unclear how the comparison between drift and selection, as causes of evolution, can be made. I have suggested conceiving of them as competing models, and testing them against a variety of the systems which are supposed to be within the domain of application. The selectionist problem is redescribed in terms of the range of applicability of selection models versus other models that could be used to describe the same systems in nature. Understanding the structure of the models helps us in comparing them; if drift models are to be compared with selection models and with combination selection/drift models, then all of the models must be framed in the same state space, i.e., aggregates of populations.

According to the above construal, a leading adaptationist claim — that natural selection is the most powerful force in evolutionary change — amounts to the claim that certain models will be successful in describing most, if not all, natural systems. Note that this does *not* entail that other processes or forces are not at work, as is sometimes assumed.

3. *Group vs. Individual Selection*

I sort through the theoretical and empirical aspects of the group selection and individual selection debate in another paper; here I wish only to make a few general points regarding the debate (manuscript, 1985).

Group selection models are population genetics models which include certain information regarding group structure and membership (see D.S. Wilson 1983 and M. Wade 1978, for detailed reviews of group selection models). Both group and organismic selection models are usually framed in terms of genotype fitnesses and frequencies. In group selection models, however, group structure is represented as well. For instance, in intrademic group selection models, the gene frequencies within each group are weighted by the size of the group. In addition, it is possible to have a model that represents both group and organismic selection (see especially Wilson 1983 for discussion).

Approaching the group selection debate from the semantic view of theories, certain substantive empirical questions facing the evolutionary biologists are immediately clear :

- 1) Does any of the group selection models describe even one

natural system more accurately than the best available individual selection model? (i.e. is a group selection model *needed* to describe accurately any system in nature?)

2) If so, what percentage of natural systems (e.g. populations, species) are best described by group selection models (of any type)?

3) Is the percentage of natural systems best described by group selection models evolutionarily significant *enough* to justify the statement "group selection plays a major or significant role in evolutionary change"?

These questions arise from consideration of group selection as an alternative description of a single system or set of natural systems. Not all biologists would agree with the above interpretation, of course.

For example, biologist Walter Bock from Columbia University, asserts that group selection hypotheses need not even be considered, since it is inevitably individuals who die. Clearly the group selection debate is not an empirical issue for Bock; he also asserts that he need not learn the details of the t-allele case in the house mouse (the only example of possible genuine group selection allowed by G.C. Williams in his classic attack on group selection, *Adaptation and Natural Selection*, 1966) (personal communication, June 1985).

Consider the controversial general claim that group selection is a relatively significant component in the process of evolution (issue #3, above). Empirical evaluation of this general claim rests on the ability to evaluate single cases. Unless the higher level generalization is being seriously considered, it might not seem necessary to evaluate competing group selection and organismic selection claims for a single set of populations. Yet, unless such comparison is performed, it is impossible to evaluate the general claim (note the similarities between this debate and the selectionist debate). D.S. Wilson complains that biologists most often do not determine the group structure measurements that would make model comparison possible in specific cases; instead, he says, they simply *assume* that group selection models are useful only infrequently (Wilson 1983). In a similar vein, Wimsatt examines cases in which researchers are biased against concluding that particular cases are best described by group selection models (Wimsatt 1980). In contrast, Wade's criticisms are theoretical, in that they concern the detailed description of the abstract system. Nevertheless, Wade's point is that the description of the abstract system has consequences for the empirical evaluation of the application of that model, both

in specific instances and in the general case (Wade 1978).

In summary, it is important to understand what sort of claim is being made in favor of group selection models. Is an empirical claim being advanced that a specific natural system is best described by a group selection model, or is it a general claim asserting the broad applicability of group selection models? The sorts of evidence needed to support these two types of claims is clearly quite different. Although the above distinctions seem quite obvious, the claims for group selection are often not distinguished by persons discussing the issues.

4. Punctuated Equilibrium

Some of the debates surrounding the controversial theory of punctuated equilibrium provide good examples of the sort of conceptual confusion that could be avoided using the framework of the semantic approach (Paul Thompson has written a detailed analysis of other aspects of the punctuated equilibrium debates using the semantic approach to theories (Thompson, manuscript)).

The theory of punctuated equilibrium is a relatively simple sort of model (see Eldredge 1971; Eldredge and Gould 1972; Gould and Eldredge 1977). The model has two main features. First, speciation by branching of lineages (as in allopatric speciation, i.e. speciation by geographic isolation, see Mayr 1963), is the primary source of significant evolutionary change, rather than the gradual transformation of lineages (i.e. phylogenetic transformation). Second, these incidents, of branching speciation are very brief in geologic time, and are followed by long periods of stasis in which the species morphology fluctuates only slightly. As Gould emphasized recently, the model describes the relative frequencies of gradual phyletic transformation and punctuated equilibrium (Gould 1983). That is, since the model is about relative frequency: any empirical claim about the model amounts to a claim about the relative frequency, one pattern — punctuated equilibrium — vs. another. The empirical claim made by Gould and Eldredge can therefore be understood as a claim about the applicability of a certain system description, intuitively, confirming the punctuated equilibrium claim requires collecting instances of the punctuated equilibrium pattern, and determining whether a high percentage of the natural systems match the punctuated equilibrium pattern better than they match the gradualist pattern.

Gould and Eldredge characterize evolution as hierarchical — it is not the result of a single process, but rather the result of different sets of processes operating to produce different aspects of evolution. I interpret this claim as follows: More than one type of model is needed to describe evolutionary systems in nature. Gould and Eldredge's specific claim is that the synthetic theory as it stands is not adequate for explaining speciation and macroevolutionary trends. This is an empirical claim — the available population genetics models *alone* are taken by the punctuated equilibrists to provide inadequate descriptions of the range of systems they are supposed to account for.

Note that this interpretation of the punctuated equilibrists' claims does not entail that punctuated equilibrium models are generally *incompatible* with gradualist models. In fact, it entails quite the opposite — ordinary phyletic evolution is taken to occur some of the time, more commonly in certain phyla or orders.

At least two questions can be asked about punctuated equilibrium models; debates about these models should distinguish between these issues:

1) How different are punctuated equilibrium models from other available models? For instance, do punctuated equilibrium models describe a pattern that is not and cannot be described by synthetic theory models? This issue involves comparing only the descriptions of the ideal systems; empirical issues are not involved.

2) How can the empirical claims about punctuated equilibrium models be evaluated? Since the empirical claims are claims about relative frequency, what sort of testing is appropriate for this frequency hypothesis? Clearly, discussion of this issue involves the well-developed field of statistical testing.

I conclude this section with a brief suggestion regarding a typical objection to punctuated equilibrium. Consider the following claim: punctuated equilibrium models assume that allopatric speciation is the predominant cause of speciation in nature; allopatric speciation is an accepted part of modern synthetic evolutionary theory, and can be represented in accepted population genetics models; therefore, since punctuated equilibrium models do not conflict with available models, they do not offer any new or valuable description of nature (see e.g. Charles Worth, Lande, and Slatkin, 1982). The distinctions discussed in this paper clarify several problems with this argument. First, the mere fact that two models are compatible does not make them equivalent. Second, the range of

application of the population genetics models is precisely what is at stake here; reasserting a claim about the range misses the point. Third, the punctuated equilibrium model describes an aggregate of systems; as such, it must be compared with what previously accepted theories say about this same aggregate. Finally, clarification of the differences in the ideal system described by punctuated equilibrium and other ideal systems should clarify the role of statistical evaluation of the empirical claims regarding these models.

Conclusion

I have discussed briefly several debates in current evolutionary theory using the semantic approach to theories as a framework. The view of explanation offered by the semantic approach allowed us to delineate various possible empirical claims regarding the theoretical models being advanced. The semantic approach to theories provides a framework that allows differences concerning the scope of application to be distinguished from differences in the description or specification of the ideal system; these differences can in turn be used to classify the various sorts of claims made about particular models. Reformulation of some key empirical and theoretical debates into the terms of the semantic view demonstrates the usefulness of the approach. I conclude that the separation of the ideal system from the empirical claims made regarding the application of that system in scientific explanation can aid in understanding some of the more complex debates confronting evolutionary biologists today.

University of California, San Diego

REFERENCES

- BEATTY, J., (1979), "Optimal-design models and the strategy of model building in evolutionary biology, *Philosophy of Science* 47: 532-561.
- BEATTY, J., (1981), "What's Wrong with the Received view of Evolutionary theory?", *PSA 1980*, Vol. II. Philosophy of Science Association, East Lansing, Mi.
- BEATTY, J., (1982), "The Insights and Oversights of Molecular Genetics: the Place of the Evolutionary Perspective," *PSA*

- 1982, vol. I. Philosophy of Science Association, East Lansing, Mi.
- BEATTY, J., (1985), "Natural Selection and the Null Hypothesis," paper delivered at the Conference on Evolution and Information, Stanford University, April 19–21, 1985.
- CHARLESWORTH, B., R. LANDE, and M. SLATKIN (1982), "A Neo-Darwinian Commentary on Macroevolution," *Evolution* 36: 474–498.
- DENNETT, D.C. (1983), "Intentional systems in cognitive ethology: The 'Panglossian Paradigm' defended," *The Behavioral and Brain Sciences* 6: 343–390.
- ELDREDGE, N. (1971), "The Allopatric model and phylogeny in Paleozoic invertebrates," *Evolution* 25: 156–167.
- ELDREDGE, N. and S.J. GOULD, (1972), "Punctuated Equilibrium: An Alternative to Phyletic Gradualism," in *Models in Paleobiology*, T.J.I. Schopf, ed.), Freeman, San Francisco
- GIERE, R.N., (1979), *Understanding Scientific Reasoning*, New York, Holt, Rinehart and Winston.
- GIERE, R.N., (1985), "Constructive Realism," In *Images of Science*, eds. P.M. Churchland and C.A. Hooker. Chicago: University of Chicago Press.
- GOULD, S.J., (1983), "The Meaning of punctuated equilibrium and its role in validating a hierarchical approach to Macroevolution" in *Perspectives on Evolution*, R. Milkman, ed.). Sunderland, M.A.: Sinauer.
- GOULD, S.J. and N. ELDREDGE (1977) "Punctuated Equilibria: Tempo and Mode of Evolution Reconsidered," *Paleobiology* 3: 115–151.
- GOULD, S.J. and R.C. LEWONTIN (1979), "The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme," *Proceedings of the Royal Society of London B* 205: 581–598.
- KITCHER, P., (1985), "Darwin's Achievement," in: *Reason and Rationality in Natural Science*, ed. N. Rescher, University Press of America.
- LLOYD, E.A., (1983), "The Nature of Darwin's Support for the Theory of Natural Selection," *Philosophy of Science* 50: 112–129.
- LLOYD, E.A. (1984), "A Semantic Approach to the Structure of Population Genetics," *Philosophy of Science* 51: 242–264.
- LLOYD, E.A. (1985), "Evaluation of Evidence in Units of Selection

- Controversies," manuscript.
- MAYR, E., (1963), *Animal Species and Evolution*. Cambridge, M.A.: Harvard University Press.
- MAYR, E., (1982), "Adaptation and Selection," *Biologisches Zentralblatt* 101: 161-174.
- SOBER, E., (1984), *The Nature of Selection*. Cambridge, MA: Bradford Books, MIT Press,
- SOBER, E., (1985), Paper delivered to the Conference on Evolution and Information, Standord University, April 19-21, 1985.
- SUPPE, F., (1972), "What's Wrong with the Received View on the Structure of Scientific Theories?" *Philosophy of Science* 39: 1-19.
- SUPPE, F., (1977), ed., *The Structure of Scientific Theories* (2nd ed.), Urbana, Ill: University of Illinois Press.
- SUPPES, P., (1957), *Introduction to Logic*. New Jersey, Van Nostrand.
- SUPPES, P., (1967), "What is a Scientific Theory ?" in: *Philosophy of Science Today* (S. Morgenbesser, ed.), New York: Meridian.
- THOMPSON, P., (1983), "The Structure of Evolutionary Theory: A Semantic Approach," *Studies in History and Philosophy of Science* 14 : 215-229.
- THOMPSON, P., "Tempo and Mode in Evolution: Punctuated Equilibria and the Modern Synthetic Theory," manuscript.
- VAN FRAASSEN, B.C., (1970), "On the Extension of Beth's Semantics of Physical theories," *Philosophy of Science* 37: 325-339.
- VAN FRAASSEN, B.C. (1972), "A Formal Approach to the Philosophy of Science," in: *Paradigms and Paradoxes* (R. Colodny, ed.), Pittsburgh: University of Pittsburgh Press.
- VAN FRAASSEN, B.C., (1980), *The Scientific Image*. Oxford: Clarendon Press.
- WADE, M.J., (1977), "An Experimental Study of Group Selection," *Evolution* 31 : 134-153.
- WADE, M.J., (1978), "A Critical Review of the Models of Group Selection," *Quarterly Review of Biology* 53 (2): 101-114.
- WILLIAMS, G.C., (1966), *Adaptation and Natural Selection*. Princeton, N.J.: Princeton University Press.
- WILSON, D.S., (1983), "The Group Selection Controversy: History and Current Status," *Annual Review of Ecology and Systematics* 14: 159-187.

WIMSATT, W., (1980), "Reductionist research Strategies and Their biases in the Units of Selection Controversy," in *Scientific Discovery: Case Studies*, ed. T. Nickles, pp. 213—259. Dordrecht: Reidel.