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Modeling Evolution in Theory and Practice

Anya Plutynski[†][‡]

University of Pennsylvania

This paper uses a number of examples of diverse types and functions of models in evolutionary biology to argue that the demarcation between theory and practice, or "theory model" and "data model," is often difficult to make. It is shown how both mathematical and laboratory models function as plausibility arguments, existence proofs, and refutations in the investigation of questions about the pattern and process of evolutionary history. I consider the consequences of this for the semantic approach to theories and theory confirmation. The paper attempts to reconcile the insights of both critics and advocates of the semantic approach to theories.

1. Introduction. In *Laws and Symmetry*, van Fraassen comments that philosophers of science have focused on the product of science, the theory, to the exclusion of the "aim, conditions, and processes of production" (1989, 189). This paper aims to fill this lacuna, especially with regard to evolutionary biology. In particular, I take a closer look at the use of models in the practice of evolutionary biology. The product/process analogy assimilates science to industry, implying that the aim of science is the production of theories, and that a strict demarcation can be made between the product, theories, and the process, scientific practice. One of the aims of this paper is to challenge this strict demarcation. I argue that the diverse types and functions of models and modeling in biology are not easily categorized as either product or process. A further aim is to consider the consequences of blurring the line of demarcation between theory and practice for the semantic approach to scientific theories.

†Send requests for reprints to the author, Department of Philosophy, University of Pennsylvania, Philadelphia, PA 19104; email: plutynski@earthlink.net.

The classic semantic view of van Fraassen (1980, 1989) characterizes theories as families of models. A theory is empirically adequate if the empirical substructures of one's "theory model" are isomorphic or structurally identical to one's "data model." So, confirmation is essentially fit between model and data. As I will demonstrate below, confirmation as identity of structure between theory and data model is inadequate to describe the ways in which many models are deployed in evolutionary biology. This paper thus follows the route of Downes (1992) and Griesemer (1990, 1991), who have each advocated a more "liberal" or "extended" semantic view of theories. They question whether isomorphism is the right way to conceive of the relation between theory and world, and whether the metamathematical sense of model adopted by the semantic view can serve as a template for all models in science.

Beatty (1981), Lloyd (1988), and Thompson (1985, 1989) have each appropriated the semantic view as a way to describe the structure of evolutionary theory. They argue that it resolves many of the problems that arise for evolutionary theory on the received, or "syntactic" view. For instance, they claim that the criticism that evolutionary theory is not a scientific theory because of its alleged lack of laws is rendered moot by the semantic view. However, Ereshefsky (1991) and Sloep and van der Steen (1987) have argued that the semantic view faces some of the same difficulties as the received view. Ereshefsky argues that the semantic approach cannot dispense with laws. Moreover, he points out that since evolutionary explanations often employ information from a number of subdisciplines within evolutionary biology, giving a formal account of their structure is forbiddingly complex, whether one adopts the semantic or the syntactic approach. In other words, the complex relation between theory and world is no less complex once one substitutes models and embeddability requirements for axioms and partial interpretation rules. Like Ereshefsky, I am skeptical that a formal account of theory and confirmation can be true to the practice of biology.

In formal approaches to characterizing the structure and confirmation of theories, such as the semantic approach, the theory-world relation is a hierarchy, with theories as fixed entities, directing practice in a top-down fashion. Nancy Cartwright (1999) calls this the "vending machine" view of theories. By contrast, she suggests that the practice of model building is a creative act, and often independent of specific dictates of theory. Likewise, Morgan and Morrison (1999) have argued that models in science may be autonomous agents and instruments of investigation. By this, I take them to mean that in the process of constructing and manipulating models, we can explore questions and discover novel empirical phenomena that are not derivable from or predicted by our best theories. I think that the views I've sketched here of Cartwright and Morgan and Morrison are

not incompatible with a more "liberal" semantic view of the sort advo-
cated by Downes and Griesemer.

   This paper will thus go some way towards attempting to reconcile the
insights of these critics and advocates of the semantic view. Evolutionary
biologists are often attempting to answer historical questions. So, testing
and deciding these questions often hinges on plausibility arguments and
existence proofs. Mathematical and material models are deployed as ar-
guments that some process or mechanism *could* be at work in nature.
Brandon (1990) has summed up this issue by describing the sort of expla-
nations often offered in evolutionary biology as "how possibly" expla-
nations. "How actually" explanations are comparatively rare. He explains
that biologists are often forced to settle for plausible scenarios, as opposed
to exhaustive explanations, given the historical character of biology, as
well as the complexity of ecological and biological systems. This point is
close to the one I wish to make about models providing plausibility ar-
guments. Often in evolutionary biology, it is more appropriate to speak
of consilience of induction by appeal to several model-arguments, rather
than confirmation via fit or isomorphism between models and world. In
what follows, I will first discuss how I think that the picture of confir-
mation offered by advocates of the semantic view might be elaborated
upon to better reflect scientific practice, and second, how three different
examples of modeling in biology serve as instruments of inquiry, existence-
proof, and model-argument, respectively.

2. On the Semantic Picture of Confirmation. E. Lloyd (1988) discusses three
forms of confirmation: fit between some model and data, independent
testing of some aspect of a model, and variety of evidence. Each of these
types of confirmation, she argues, is a variant of the same general type:
demonstration that a natural system is isomorphic in certain respects to a
model. While I think that Lloyd's account is the best we have yet of how
evolutionary hypotheses are confirmed, I wish to suggest the following
emendations of her view.

   Isomorphism, while it may be an ideal relation between model and
world, is often neither hoped for nor possible, in evolutionary biology.
Lloyd mentions this point in a footnote (1988, 168), but I think that this
issue calls for greater elaboration. Many models are simulations of natural
systems. While one hopes to incorporate as much realism as possible in
such cases, laboratory or computer simulations will necessarily be very
different from natural systems. In fact, it is exactly when a process in
nature is too complicated to track, or would take too long to observe, that
such simulations are appropriate. Biologists do not expect such simula-
tions to be isomorphic to natural systems. Rather, simulation models serve
in both an exploratory and argumentative role. A simulation can yield

new empirical results, or suggest that one or another factor in the evolutionary process is more or less significant. I will discuss an elegant example below of a simulation of 20,000 generations of evolution using *E. coli* as an experimental system.

Modeling in biology often has the role of demonstrating the plausibility of some process or mechanism. While Lloyd mentions this point in her discussion of Beckner, I believe that this important function of modeling in biology gets left to one side in her subsequent discussion. Sometimes, the question is not whether one can generate a model whose assumptions are well confirmed or whose results have a good fit with empirical data, but whether one can generate a model at all that is just robust *enough* to give us good reason to expect that some process could occur in nature. Success at constructing such a model can serve as an existence proof. Rice and Salt's (1988) model of speciation in sympatry is one example (see below).

Lloyd devotes some discussion to the problem of counterfactual assumptions or idealizations—we are warned to be skeptical of models that employ such assumptions. I agree. However, I would argue that there are some cases where this skepticism ought to be suspended. There are an enormous number of factors at work in any evolutionary process. To incorporate all these factors in a model would quickly make our mathematics intractable. Counterfactual assumptions are thus par for the course in modeling evolutionary dynamics. Infinite population size, haploidy, or random mating, are often unavoidable, if counterfactual, assumptions one needs to make in order to answer specific evolutionary questions. Proponents of the semantic view argue that models are abstract and often involve idealization. Theoretical hypotheses serve as an empirical interpretation of theoretical models, namely, that the model is isomorphic in some respect to the world. However, this brief story sidesteps one of the most interesting aspects of the interpretation and evaluation of models and modeling: which kind of idealizations are appropriate in which contexts and why. While I cannot hope to provide an exhaustive answer to this question here, I'll suggest the following. The question of independent support for one or another assumption is sensitive to the kind of questions one is addressing. Moreover, there is a fundamental trade-off at work in deciding upon model assumptions: how much are you willing to sacrifice in explanatory detail in exchange for a general and tractable answer to some evolutionary question? The amount of risk one takes in ignoring complicating factors is directly proportional to the gain in degree of generality of one's model. In some cases, assuming an infinite population size or random mating is appropriate; it depends both on the context and the risk one is willing to assume. This may seem counterintuitive: how can models serve as plausibility arguments when the assumptions of the model

are so implausible? For example, infinite population size is simply an impossibility. Oughtn't we regard any model assuming this to be suspect? Certainly, counterfactual assumptions may give us reason to doubt the plausibility of a model argument. However, in many cases, models that are simply false can often be as effective, if not more effective, in furthering theory as those models that are true of or similar to the world are (Wimsatt 1987). If we were to reject any model argument with counterfactual assumptions, then we would have to side with Pearson and Punnett in their initial rejection of Fisher's (1918) paper, where he argued for the compatibility of biometry and a gradualist picture of evolution with the principles of Mendelism. Counterfactual assumptions are not always reason to regard a model as suspect. In some cases, a model that employs counterfactual assumptions can serve as a compelling argument, either for or against the possibility of some relation, pattern, or process in nature. I will give an example below from a debate over the founder model of speciation.

According to the classic semantic view, mathematical models are abstract representations of real systems. Laboratory experiments will serve to generate data models, which are then checked against one's theory model. This top-down picture takes mathematical models to be the core expression of theory, and laboratory models to be testing grounds for one's theoretical hypotheses. In the practice of science, this hierarchy is often reversed. Mathematical models often serve as tools for investigation; the investigative aspect of science is not confined to the lab or field. Mathematical or computer simulation models can function as tests of theoretical questions in the same way as do laboratory experiments. Moreover, there is an interesting division of labor in terms of the scope of question capable of being investigated in mathematical versus laboratory modeling. Mathematical models can serve to answer questions that cannot be addressed in a laboratory model, and vice versa. In the examples discussed below, mathematical and material models serve as independent, complementary lines of evidence in addressing questions about the pattern and process of evolution, rather than steps in a hierarchy between theory and world.

3. Some Models of Models. Now I will consider three examples of modeling which illustrate the instrumental and argumentative role of diverse types of models in biology. J. Griesemer (1990) has recently brought attention to the role of material models in evolutionary biology. Richard Lenski conducted an experiment using *E. coli* to investigate the dynamics of evolution over many generations. *E. coli* have a generation time of about twenty minutes under optimal conditions, yielding many generations a day, and can be transferred into fresh medium and frozen at $-80°C$ with-

out damage. This makes them analogous to "machines for time travel" for the study of processes of evolutionary change (Lenski and Travisano 1994). Lenski and Travisano describe such a system as follows:

> Imagine that you have discovered a well-preserved and clearly strat- ified fossil bed that provides a record of evolution extending thou- sands of generations for the particular organism that you study. . . . Imagine that you could resurrect these organisms and reconstruct their environment exactly as it was during thousands of generations preserved in the fossil bed. . . . You could travel back in time and manipulate populations by altering their evolutionary history or their environment, and then return to the present to examine the effect of these conditions on the dynamics of adaptation and diversification. (1994, 6808–6809)

Lenski and others have been conducting a long-term evolution experiment on twelve replicate populations of *E. coli* culture with frozen records of approximately 20,000 generations. Fitness (measured as the ratio of the number of doublings of derived vs. ancestor strains) of twelve replicate populations increased by approximately 45%, with most improvement taking place in the first 2000 generations. The trajectory of mean fitness for the twelve strains approximates an asymptotic curve, suggesting that there are constraints on indefinite improvement. The system allows one to investigate the dynamics of adaptation in populations, the relative signif- icance of stochastic factors, and other evolutionary questions, since each stage in the process is preserved. Lenski's simulation model is not simply an experiment which can confirm one or another hypothesis about evo- lutionary dynamics. He uses it as an investigative tool, i.e., as a source of new questions as well as answers about the evolutionary process. At 20,000 generations, Lenski and his students are discovering new information about the dynamics of evolutionary change. In particular, several of the strains acquired a mutation, which caused them to have an elevated mu- tation rate. These strains can be put into competition with other strains, or manipulated using molecular techniques, to address questions about the evolution of mutation rates: Is there an upper or lower limit on the rate of mutation? What constrains that limit? In other words, Lenski's model is a fruitful source of new questions and potential experiments. Moreover, Lenski has used his system to argue that the divergence in relative fitness of strains (see Figure 1), all resulting from a common ancestor, suggests that drift plays a significant role in the evolutionary process.

Another such material model is the 'speciation machine' constructed by Rice and Salt (1988; see Figure 2). Rice and Salt constructed a labo- ratory model similar to Lenski's which they claim demonstrates the effec- tiveness of speciation in sympatry, i.e., within an interbreeding population.
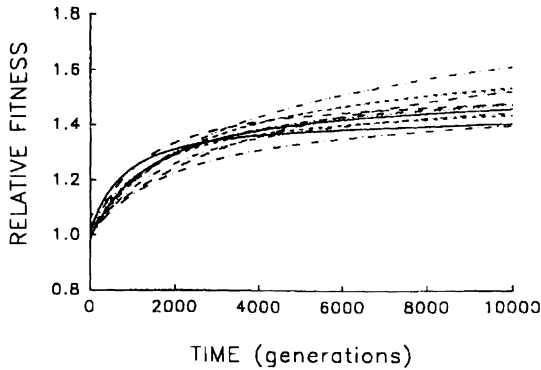
Figure 1.   Lenski et al.'s (1994) trajectories of mean fitness relative to the ancestor in 12 replicate populations of *E. coli* during 10,000 generations of evolution in the laboratory.

Their long-term experiment was able to generate several reproductively isolated strains of *Drosophila* through sympatric means, via disruptive selection by habitat specialization. They constructed a habitat maze where *Drosophila* chose selective habitats that differed with respect to light, gravity, and choice of chemical vapors. Positive assortative mating evolved as a correlated response to the disruptively selective character, in this case, preference for different habitats within the maze. Key to this experiment is that selection alone was able to generate isolated strains. There were no population bottlenecks or isolation; each entire generation of flies from the several habitats were returned together to the beginning of the maze and allowed to choose their habitats.

This is only one among many experiments with laboratory populations of *Drosophila* that have been used to investigate different hypotheses about speciation. There has been at least forty years of work on speciation in the lab. *Drosophila* are the organism of choice, and there have been tests of selective divergence, founder effect, and sympatry (for a review, see Rice and Hostert 1993). Rice and Salt's work challenges what has been the received view among evolutionary biologists, namely that geographical or spatial isolation is a crucial condition for speciation, and that directional selection alone cannot generate new species. The mainstream view for approximately fifty years among evolutionary biologists is that speciation in allopatry (geographical isolation) is the major mode of speciation, and that founder effect (the isolation of a small subpopulation and reconstitution of the genetic architecture through drift) is one of the most common means of speciation. Rice and Salt's model serves as an argument to the contrary. Their laboratory model thus serves as an existence proof that speciation can occur in sympatry.
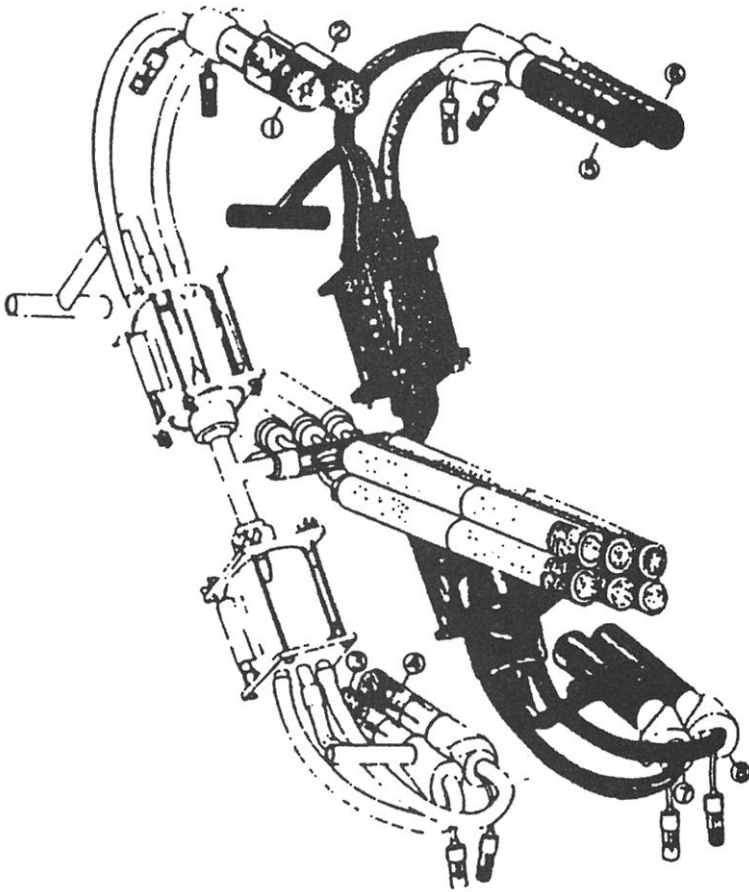
Figure 2.   Rice and Salt's (1988) *Drosophila* habitat maze for speciation in sympatry. Positions of the selective habitats are indicated by number (1–8).

Several questions arise out of this material modeling of the speciation process. For example, how relevant are laboratory experiments to speciation in the wild? Some might question the relevance of Rice and Salt's experiment to natural speciation processes. Others claim that laboratory populations are fundamentally different from natural populations, and therefore laboratory experiments and breeding experiments are irrelevant to the problem of how new species arise. This argument is in the tradition of naturalists such as Jordon and Kellogg (1907), who claimed that no product of the botanical garden as a result of breeding experiments could count as a case of speciation.

Additionally, how are we to evaluate the results of these speciation experiments? How isolated is 'reproductively isolated'? Must one show

complete reproductive incompatibility? Is lowered viability and fertility in attempted crossing sufficient? When are two organisms truly new species? Rice and Salt showed that their sympatry experiment yielded populations with lowered viability and assortative mating: Is this a speciation event?

Clearly, inferences from the laboratory to the wild are not decisive. Laboratory work is not meant to reproduce all factors relevant in nature. Rather, one or several parameters—e.g., selection by habitat type, drift, etc.—can be tested either individually or in combination or competition with one another. Models such as Rice and Salt's are not decisive tests so much as supplementary lines of evidence. The standard top-down picture of theoretical models being confirmed by laboratory or fieldwork is not appropriate here. The theory of sympatry is not confirmed by identifying isomorphisms between the laboratory data and the theory model. Rather, the very fact that Rice and Salt were successful at constructing simulation of speciation in sympatry serves as an argument for its occurring in nature. In evolutionary biology, often simply demonstrating the possibility of some process in the lab is a persuasive case for its occurrence in nature. In this case, lowered viability in crosses of these lab strains is an argument for the possibility of sympatry in the wild.

Multiple lines of evidence from multiple different subdisciplines within evolutionary biology bear on the question of how important, for instance, drift is in evolution, or which mode of speciation is possible or prevalent in nature. Evolutionary questions are almost never decided by single "crucial experiments." Biologists construct models such as Lenski's and Rice and Salt's not to *prove* the relative significance of one or another factor in the evolutionary process, but to provide a plausibility argument. In this sense, a laboratory experiment functions in the same way as some theoretical or mathematical models in population genetics. Mathematical models can serve as arguments as well. Moreover, mathematical models can answer questions that laboratory models cannot.

For example, another line of evidence on the role of founder effect in speciation is theoretical population genetic models. Two self-professed neo-Darwinians, Barton and Charlesworth (1984), devoted a review paper to theoretical objections to the founder model. They concluded that although founder effects may cause speciation, they are only a very rare extreme along a continuous range of possibilities. Complete geographic isolation is unnecessary, and selection can break up coadapted systems of alleles. In particular, they question the "genetic revolution" as a mechanism of speciation, and argue that speciation is more likely the result of small steps than a single founder event.

While the theoretical arguments are too mathematically complex to reproduce here, Barton and Charlesworth show how under both single- and multi-locus models, reduction in variability induced by drift reduces the chances of peak shifts, i.e., the transition from one equilibrium under

selection to another. Selection requires variability to act upon. Loss of heterozygosity during a founder event reduces that variability. Mayr (1942, 1963, 1970) argued that reduction in population size was key to speciation, in that such a reduction would entail an exposure of new gene combinations because of a loss of heterozygosity. The resulting transformation of the genetic composition of a population has been called a "genetic revolution." Barton and Charlesworth counter that the loss of heterozygosity can occur only in populations that grow so slowly that they are more likely to die out than evolve into new species. They also explain that the probability of peak shifts—moving from one peak on Wright's adaptive landscape to another— decreases exponentially with the size of each step. In other words, the probability that a founder population will undergo a rapid transition to a new selective equilibrium is very low. Reproductive isolation is more likely to evolve in a series of small steps than in a single "genetic revolution." Their mathematical model serves as an argument against the founder effect, or more specifically, "genetic revolutions" playing a role in speciation.

One might argue that the classic semantic view is still appropriate for these examples. For instance, the habitat maze is a structure that is true for, or satisfies, the sentences of the theory of sympatry. However, the usefulness of this metamathematical sense of model is stretched to the limit when it comes to describing how such models function in the practice of evolutionary biology. Models such as Rice and Salt's habitat maze, or Barton and Charlesworth's mathematical model of peak shifts, are not confirmations, nor are they theoretical models that await confirmation. The laboratory model is a caricature of what actually goes on in natural populations. Laboratory models such as Rice and Salt's function simultaneously as a tool for investigation and a test of the plausibility of one mechanism of speciation. If sympatry were possible, how would it work? And, can we make it work? Barton and Charlesworth's model functions as an argument, not a theory that awaits testing in the lab or field. Multiple different types of models which jointly establish the plausibility of the same mechanism yield a consilience of induction in favor of its existence in nature. Confirmation in historical disciplines such as evolutionary biology is rarely a matter of simply checking the fit between model and world. Because we can rarely see evolution in action, evolutionary biologists use models as tools for investigation, existence proofs, and arguments for or against the plausibility of one or another mechanism at work in nature.

4. Conclusion. Biologists more often than not resort to laboratory simulations and idealized mathematical models as sources of plausibility arguments. Moreover, models and modeling can have multiple, diverse func-

tions, which are not easily characterized as either theory making or confirmation. Models can yield new questions or empirical phenomena not predicted by theory, serve as existence proofs, or as arguments for or against the significance of one or another mechanism at work in nature. While the appropriation of formal semantics was a helpful way to get out of the rut of viewing theories as sets of axioms, the semantic view still carries the taint of the discovery-justification divide. In evolutionary biology, discovery and justification, along with theory and practice, are not so easily demarcated. Models and modeling are not ancillary to theory, but can function as independent tools for investigation.

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