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**UNDERDETERMINATION
AND MODELS IN BIOLOGY**

Abstract: *Since the early 20th century underdetermination has been one of the most contentious problems in the philosophy of science. In this article I relate the underdetermination problem to models in biology and defend two main lines of argument: First, the use of models in this discipline lends strong support to the underdetermination thesis. Second, models and theories in biology are not determined strictly by the logic of representation of the studied phenomena, but also by other constraints such as research traditions, backgrounds of the scientists, aims of the research and available technology. Convincing evidence for the existence of underdetermination in biology, where models abound, comes both from the fact that for a natural phenomenon we can create a number of candidate models but also from the fact that we do not have a universal rule that would adjudicate among them. This all makes a strong case for the general validity of the underdetermination thesis.*

Keywords: *underdetermination; model building and selection; curve-fitting problem*

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**Nedourčenost
a modely v biologii**

Abstrakt: *Nedourčenost je jedním ze zásadních problémů filosofie vědy od počátku 20. století. Ve svém příspěvku vztahuju tezi o nedourčenosti k biologickým modelům a obhajuju následující dva argumenty: Za prvé, použití modelů v této disciplíně dodává silnou váhu tezi o nedourčenosti. Za druhé, modely a teorie v biologii nejsou determinovány striktně logikou reprezentace studovaného jevu, ale také dalšími faktory, jako jsou výzkumné tradice, background vědců, cíle výzkumu a dostupné technologie. Přesvědčivý důkaz o existenci nedourčenosti v biologii, která modelů v hojně míře využívá, pramení nejenom z faktu, že pro každý přírodní jev můžeme vytvořit velký počet alternativních modelů, ale také z faktu, že nedisponujeme univerzálním pravidlem pro výběr mezi nimi. To vše mluví ve prospěch platnosti teze o nedourčenosti.*

Klíčová slova: *nedourčenost; vytváření a výběr modelů; proložení dat křivkou*

Underdetermination is a contentious issue in the philosophy of science. Since the inception of the problem by Duhem¹ and Quine,² which was later somewhat inaccurately dubbed the Duhem-Quine thesis, the original question has been discussed in various contexts in the philosophy of science and has also arisen in other disciplines. While Duhem remained within the confines of (physical) theory, Quine with his concept of the “web of belief” canvassed an all-encompassing version of epistemological underdetermination. Later philosophers took opposing stances regarding the problem (for example Laudan³ and van Fraassen⁴) with each camp mounting evidence for and against the existence of the phenomena or its importance. Adherents, who point out that underdetermination is an intrinsic feature of scientific theories that cannot be eradicated, often harness underdetermination to support their own philosophical positions (Feyerabend, Kuhn). On the other hand, critics including Laudan dismiss most types of underdetermination on the grounds of its unimportance for science, and consider the whole problem of underdetermination “overplayed”, especially by its modern day advocates such as STS and SSK theorists.⁵ Most philosophers usually fall somewhere between the extremes and hold the moderate view that underdetermination does exist in one form or another.

The central tenet of underdetermination, that our theories are underdetermined by available empirical data, has over the years ramified into a rich family of related concepts: Besides the general thesis of underdetermination, which comes in “strong” and “weak” variants,⁶ other concepts have been proposed, such as ampliative underdetermination,⁷ transient underdetermination,⁸ empirical or observational equivalence⁹ local under-

¹ Pierre Duhem, *The Aim and Structure of Physical Theory* (New York: Atheneum, 1905).

² Willard Quine, “Two Dogmas of Empiricism,” *Philosophical Review* 60, no. 1 (1951): 20–43.

³ Larry Laudan, “Demystifying Underdetermination,” in *Scientific Theories*, ed. Wade C. Savage (Minneapolis: University of Minnesota Press, 1990), 267–97.

⁴ Bas van Fraassen, *The Scientific Image* (Oxford: Oxford University Press, 1980).

⁵ Laudan, “Demystifying Underdetermination,” 267–97.

⁶ For example, in Thomas Bonk, *Underdetermination: An Essay on Evidence and the Limits of Natural Knowledge* (Dordrecht: Springer, 2008).

⁷ Laudan, “Demystifying Underdetermination,” 267–97.

⁸ Lawrence Sklar, “Methodological Conservatism,” *The Philosophical Review* 84, no. 3 (1975): 374–400.

⁹ Larry Laudan and Jarrett Leplin, “Empirical Equivalence and Underdetermination,” *The Journal of Philosophy* 88, no. 9 (1991): 449–72.

determination¹⁰ and a host of others.¹¹ Underdetermination is also, directly or indirectly, present in many current debates on realism and antirealism, induction, and the like. And underdetermination (and overdetermination) are also basic concepts in statistical and mathematical modeling and as such have a direct impact in a number of scientific disciplines both in the natural and social sciences.

The fact that underdetermination comes in different shapes and sizes also means that the original concept has been to some degree obfuscated and has lost its initial focus. Since the evolution of the concept and the ensuing debates about it are covered in a number of books and articles,¹² I will narrow my focus and concentrate on a specific problem in the current debate – underdetermination in model building and selection in biology – which can be addressed within the limited scope of this article, and which, nevertheless, has implications for the general thesis.

Underdetermination and Models

In many sciences it is a commonplace that for any given natural or social phenomenon there are a number of legitimate ways to create its representation. For empirical observations or experimental data we can build (theoretically) an indefinite number of models relating to diverse underlying theories and concepts. Through this connection, the concept of underdetermination is closely linked to model building and model selection. In statistical modeling, scientists work with a limited set of observations, for which an unlimited number of models can be inferred. Immediately therefore the question arises as to how we decide which model out of this set of candidate models we should choose, and what is the justification for such a choice.¹³ This can also be articulated as the “curve fitting” problem, i.e., the task of fitting

¹⁰ Derek Turner, “Local Underdetermination in Historical Science,” *Philosophy of Science* 72, no. 1 (2005): 209–30.

¹¹ There are, of course, more classifications available, such as moderate and radical underdetermination, etc. Cf. Seungbae Park, “Philosophical Responses to Underdetermination in Science,” *Journal for General Philosophy of Science/Zeitschrift für allgemeine Wissenschaftstheorie* 40, no. 1 (2009): 115–24.

¹² For a short introduction see Stanford Kyle, “Underdetermination of Scientific Theory,” in *Stanford Encyclopedia of Philosophy*, accessed December 27, 2016, <https://plato.stanford.edu/archives/spr2016/entries/scientific-underdetermination/>.

¹³ I. A. Kieseppä, “Statistical Model Selection Criteria and the Philosophical Problem of Underdetermination,” *The British Journal for the Philosophy of Science* 52, no. 4 (2001): 761–62.

a curve through data points.¹⁴ Intuitively, we can see that there are infinitely many curves that can agree with the data, but we are challenged to pick only one of them. At this point it is also apparent where this issue touches on the long-standing problem of induction in the philosophy of science. In the case of deterministic modelling, scientists face an almost identical challenge because there are usually a number of candidate models at hand. Thus, historically, whole branches of mathematics and statistics are concerned with modelling and model selection.

However, if we closely scrutinize the problem of the selection of the models, we will soon see that the entire process is not only carried out with formally devised and executed methods, but also involves, on the part of the modeler, some subjective decisions which usually depend on his or her own scientific or philosophical leanings and other factors such as the circumstances of the research.

In this article, the problem of underdetermination is demonstrated with examples from the biological sciences. There are several reasons for this. First, models in biology are so widespread that the topic is not merely a theoretical exercise but has many real-life examples with practical implications. Second, due to the advanced formalization of model building and selection procedures in biology we have the advantage of a clear exposition of the issues related to underdetermination. The high level of formalism helps to clarify the outstanding problems which are a part of model construction and selection and which tend to be rather obscured in the general philosophical discourse.

Models in Biology

Models are now ubiquitous in many scientific disciplines including the life sciences.¹⁵ Generally, models can be defined as “abstractions or simplifications of a real-world system.”¹⁶ But if we try to find a universally accepted definition of a model we encounter a plethora of propositions that usually reflect the author’s own underlying philosophical positions. For example, the semantical view conceives of models as entities that in some simplified

¹⁴ Aris Spanos, “Curve Fitting, the Reliability of Inductive Inference, and the Error-Statistical Approach,” *Philosophy of Science* 74, no. 5 (2006): 1046–66.

¹⁵ Hiroaki Kitano, “Computational Systems Biology,” *Nature* 420, no. 6912 (2002): 206–10.

¹⁶ Mark L. Taper, David F. Staples, and Bradley B. Shepard, “Model Structure Adequacy Analysis: Selecting Models on the Basis of Their Ability to Answer Scientific Questions,” *Synthese* 163, no. 3 (2008): 358.

way represent the target system with a relationship of isomorphism, partial isomorphism or, less restrictive, similarity.¹⁷ For philosophers, the character and scope of models in science is a matter of dispute, so we will find a host of other definitions too. As the exact nature of the model–world relation is not so important for the general thesis that I advance in this article, I will adhere to the liberal definition given in the beginning of this paragraph that covers the most common uses of the term in the sciences, including biology, for which I will provide concrete examples of models representing real natural phenomena.

There is one important point here, however, that concerns the relations between models and theory. It is sometimes argued, particularly by those who subscribe to the semantic view of theories, that models are instantiations of a general theory.¹⁸ In this framework, the theory can be conceived of as a family of models, (i.e., a generalized version of particular real models). We can usually make such a distinction for some models in physics, where a particular physical system (such as the Solar system) is an instantiation of a general theory (Newton's laws). Although I consider this to be a valid point of discrimination, in biology such a clear-cut distinction between theories and models cannot easily be made. One reason is linguistic, since in biology the terms “model” and “theory” are often used interchangeably.¹⁹ Quite often the generalizations in population dynamics, from which I draw my next example, are routinely referred to both as models and theories. So the boundaries here are obviously blurred.²⁰

¹⁷ Frigg comes up with a simple three-way classification: representational models of phenomena, representational models of data, and models of theory, but we can also find other proposals. The examples in this article fall into the first two categories, which are – in my view – non-exclusive. Representational models of phenomena cover “all relatively stable and general features of the world that are interesting from a scientific point of view”. Representational models of data are “corrected, rectified, regimented, and in many instances idealized version of the data we gain from immediate observation, the so-called raw data”. Models of theories have their origin in logic and conceive of models as instantiations of a theory (closed set of sentences in a formal language). See Roman Frigg and Stephan Hartmann, “Models in Science,” in *Stanford Encyclopedia of Philosophy*, accessed December 27, 2016, <https://plato.stanford.edu/archives/win2016/entries/models-science/>.

¹⁸ Roman Frigg, “Models in Physics,” in *Routledge Encyclopedia of Philosophy*, accessed December 27, 2016, <https://www.rep.routledge.com/articles/thematic/models-in-physics/v-1>.

¹⁹ Frigg also makes this point for some of the physical theories and models, where the two cannot be clearly distinguished (in particle physics).

²⁰ For example, Berryman in his article discusses “predatory-prey theory”, whereas in other articles Wangersky, Berryman, Gutierrez and Arditi use term “predatory-prey model”. See Alan A. Berryman, “The Origins and Evolution of Predator-Prey Theory,” *Ecology* 73, no. 5

Even if we adopt the view of models as constituents of a more general theory, there is also an epistemological reason why this is not possible: Suppose we construct a model for a phenomenon in biology; subsequently we can build a more abstract model that applies to more phenomena and so forth. It is then not clear when the models become general enough to form a theory and stop being just models, since we can almost always abstract to a more general entity. This is why the model-theory dichotomy doesn't hold, at least for the cases listed in this article. Because generality is also an important feature of models – as we will see – it is important to clarify this issue at this point before I continue in the exposition of the problem.

What I mean by models in biology will be demonstrated with the following real-world example of a lake ecosystem.

One of the models routinely used in biology is the one depicting the interactions of species with the environment. In this case, researchers built a model of the lake ecosystem of Loch Leven in Scotland with a special interest in mind – they investigated the combined effects of eutrophication and climate change on the quality of the water.²¹ The quality of water is measured by the level of algal biomass – a smaller level of nutrient pollution means lower levels of phytoplankton biomass. In the Loch ecosystem, one of the relationships has a predatory-prey character, because water-fleas (*Daphnia*) graze on the algae. Therefore due to this close dependence, the quantity of zooplankton can also be considered an indicator of water quality. Based on previous results, the researchers suggested which variables should be included in the models that would faithfully capture the key relationships in the lake ecosystem. Due to the complexity of the ecological system the researchers employed several techniques: transfer functions, additive models, and varying-coefficient models to deal with the lagged relationships and to explore non-monotonic trends, seasonality and relationships among variables. The models made use of the following variables: nutrients (soluble reactive phosphorus – SRP, and nitrate-nitrogen – $\text{NO}_3\text{-N}$), zooplankton or water-fleas (*Daphnia*), water temperature, and chlorophyll-a (algal biomass), with chlorophyll-a and zooplankton considered the response variables. They built several different models of relationships between variables as

(1992): 1530–35; Peter J. Wangersky, “Lotka-Volterra Population Models,” *Annual Review of Ecology and Systematics* 9 (1978): 189–218; Alan A. Berryman, Andrew Paul Gutierrez and Roger Arditi, “Credible, Parsimonious and Useful Predator-Prey Models: A Reply to Abrams, Gleason, and Sarnelle,” *Ecology* 76, no. 6 (1995): 1980–85.

²¹ C. A. Ferguson et al., “Model Comparison for a Complex Ecological System,” *Journal of the Royal Statistical Society. Series A (Statistics in Society)* 170, no. 3 (2007): 691–711.

well as a combined model. In the first step they tried to identify lagged relationships with the automatic identification procedure SMISO (Seasonal Multiple Input Single Output), which employs the Gauss-Newton iterative stepwise algorithm for the computation, and uses the Bayesian information Criterion (BIC) to select the most appropriate one. Further, they went on to build varying-coefficient models and additive models, for which they used F-statistics (classical hypothesis testing) to select among the models.

What can be learned from this modelling exercise? As the authors conclude, in a complex ecological system such as Loch Leven, a variety of models are required to account for the web of relationships in the system.²² Although the authors built more than a dozen models they still suggested further refinements that would bring more accuracy or a more realistic representation of the processes in the Loch. Among the possible improvements would be to consider *Daphnia* and algae as a combined (instead of individual) response, and to construct multivariate models which would include external variables other than water temperature.

This simple example fully illustrates the intricacies accompanying model building.²³

One decision that has to be made is which variables should be included in the picture. The authors admit that the number and type of variables in the model was based on previous knowledge so the necessary exploratory work had been done. To keep the model simple they selected only five variables out of 150 that they had at their disposal, and the rest – covering other chemical, biological and climatic features of the lake – were left out. More parameters (variables) in the model would increase its precision (goodness-of-fit) but would come at the expense of the parsimony of the model and

²² Ibid., 709.

²³ The situation in which scientists have multiple candidate models is far from rare in biology, but rather constitutes a widespread pattern. For example, in one project, scientists sought to identify the factors that influence density levels of cutthroat trout (*Oncorhynchus clarki lewisi*) and brook trout (*Salvelinus fontinalis*) in Montana streams – native and invasive species respectively. Scientists modelled the levels of the fish in their habitat with the help of 38 abiotic and biotic (including anthropic) variables such as elevation, slope, aspect, latitude, longitude, stream size, and bed type, and anthropic factors such as the levels of grazing, mining, and logging, which were further reduced into 8 factors. After they included interactions and quadratic terms in the model they ended up with dozens of credible candidate models, a situation which required the choice of selection criteria on which they would need to base their decision. See Mark L. Taper, “Model Identification from Many Candidates,” in *The Nature of Scientific Evidence: Statistical, Philosophical, and Empirical Considerations*, ed. Mark L. Taper and Subhash R. Lele (Chicago: University of Chicago Press, 2004), 488–524.

its explanatory power, which would thus hinder the understanding of the crucial relationships in the ecosystem.

From this example it ensues that the study of biological phenomenon usually entails creating multiple models, which, as with any generalizations, never capture all the details, but selectively reflect a mere portion of the underlying reality.

How to Choose a Model?

With a number of candidate models at hand, scientists have to decide which one best satisfies their criteria. One of the most common questions is whether they prefer parsimony or goodness-of-fit in the model, because not all of these “desiderata”²⁴ are attainable at the same time, which means that during the selection process they must accept tradeoffs of some kind. Scientists usually obtain a closer fit to the data when the model has more parameters but this is at the expense of its simplicity and of the intelligibility of the more complex model.

In statistical modelling, the tradeoff between the parsimony (simplicity) of the model and its goodness-of-fit has an exact expression.²⁵ When choosing the models of the relationships in Loch Leven, the researchers took advantage of several model selection methods, such as the Bayesian information Criterion (BIC) and classical hypothesis testing (F-statistics) which can quantify these tradeoffs.

These two measures are not the only ones as statisticians have developed a number of methods of model selection – in addition to classical hypothesis testing (Neyman-Pearson) and Bayesian information criterion (BIC), there are the maximum likelihood method, minimum description length method, cross-validation techniques and Akaike’s information criterion (AIC) – all of which provide a measure of balance between the goodness-of-fit and parsimony of the model, although each of them has different merits and underlying conceptual ideas.²⁶

²⁴ “Desiderata” is a term coined by Levins. See Richard Levins, “The Strategy of Model Building in Population Biology,” *American Scientist* 54, no. 4 (1966): 431.

²⁵ More about parsimony in Kenneth P. Burnham and David R. Anderson, *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (New York: Springer-Verlag, 2002), 443.

²⁶ The overview of these methods can be found in Burnham, *Model selection and Multimodel Inference*, 2–3, or in Forster, “Key Concepts in Model Selection: Performance and Generalizability,” 205.

How these particular measures work will be illustrated with the example of Akaike's Information Criterion (AIC)²⁷ based on the information theory, which also measures the trade-offs between the parsimony and the goodness-of fit of the model to the data. The AIC is calculated in one of the following ways:

Using the maximum likelihood estimate (L) and the number of model parameters (k)

$$\text{AIC} = -2 \ln(L) + 2k,$$

or, alternatively, using the residual sum of squares of the model (RSS), sample size (n), parameters of the model (k), and assuming normal distribution

$$\text{AIC} = n [\ln(\text{RSS} / n)] + 2k$$

As can be read from the equations, AIC rewards the fitness of data (sum of squares) but penalizes adding extra parameters (k) into the model. AIC is a relative measure; a lower value for a model indicates that from a set of candidate models, this model has the fewest parameters which are still an adequate fit to the data.

All the methods mentioned above differ in respect to how they can be used and what they express. For instance, classical hypothesis testing can only be used for nested models,²⁸ whereas AIC and its derivatives can compare both nested and non-nested models. As to the balance between goodness-of-fit and complexity of the models, AIC penalizes the complexity of the model as measured by number of parameters more than Bayesian Information Criterion (BIC), etc. On the other hand, AIC only compares models relatively to the set of candidate models and doesn't measure the overall fit to the data.

When applied, these model selection procedures give varying results as different models are singled out as "best" by the procedures. As Forster remarks, the matter is far from settled and there is "considerable disagreement" when it comes to application of selection methods among the theorists,²⁹ and therefore there is no universal criterion that would be preferred by the scientific community. More selection methods also bring other factors into

²⁷ First proposed by Hirotugu Akaike in 1973. In Hirotugu Akaike, "A New Look at the Statistical Model Identification," *IEEE Transactions on Automatic Control* 19, no. 6 (1974): 716–23.

²⁸ Nested models are those that are related, i.e., one is the simpler case of the other.

²⁹ Forster, "Key Concepts in Model Selection: Performance and Generalizability," 216, 229.

play such as the context of the research and the underlying beliefs of the scientists. And it goes without saying that working with different models when they are taken as a representation of underlying reality can have serious practical implications.

Deterministic Models in Biology

In other areas of biology the situation is similar, for example deterministic models of population dynamics (predator-prey) often have to balance opposing requirements and vacillate between goodness-of-fit and parsimony, and other desiderata. As in other areas, a multiplicity of models in population dynamics is commonplace. In their overview of the current state of population biology, Berryman, Gutierrez and Arditi present more 27 types of predator-prey models.³⁰ Apart from the original Lotka and Volterra models from 1926 and 1928 respectively, they list a number of other models with their characteristics: mass-action models, prey-dependent functional response models, logistic ratio-dependent functional response models, etc.,³¹ and they also discuss the suitability of each type of model and the conditions under which they can be applied including their advantages and drawbacks. All these models vary in regard to their generality, parsimony, time scales or purpose for which they have been built, and this determines their utility in a particular research situation. The scientist-modeler always has to confront the challenge of how sophisticated the model should be, how many relationships and of which type should be included or omitted and other factors.

This problem cannot be easily remedied. As population biologist Levins stated in his landmark paper “The Strategy of Model Building in Population Biology,”³² the challenges that a scientist-modeler in population biology has to address come from the fact that the scientist has to simultaneously take into account various kind of heterogeneity (physiological, and age) in the multiple species involved in the model. Moreover, biological systems are subject to continuous changes as a result of influences of other species

³⁰ The classical Lotka-Volterra model depicts prey-predator dynamics with the following differential equations: $dx/dt = \alpha x - \beta xy$, $dy/dt = \gamma xy - \delta y$, where x is the number of prey organisms, y is the number of predator organisms, and α , β , γ , δ are parameters describing the interaction of the species.

³¹ Berryman et al., “Credible, Parsimonious and Useful Predator-Prey Models,” 1982.

³² Levins, “The Strategy of Model Building in Population Biology,” 421.

and of the environment.³³ How can we deal with such a complex system, asks Levins? An extremely precise mathematical model which would try to capture the network of existing relationships “would require using perhaps 100 simultaneous partial differential equations with time lags; measuring hundreds of parameters, solving the equations to get numerical predictions, and then measuring these predictions against nature.”³⁴ Such a gargantuan task was intractable in Levins’ day, since the equations would not be solvable analytically and the limited power of computers at the time rendered even approximate solutions difficult to obtain.

As a result, building such models of relationships in biology again involves navigating the treacherous waters of tradeoffs. Models exhibit either parsimony, or precision, or other scientific virtues (desiderata) such as generality, but not all of them at the same time. The fact that these virtues cannot be upheld simultaneously also shows that the performance of the models vary in concrete situations as their aptitudes for a particular use. Also, these distinctions cannot on the whole be simply explained away by the reality that is modelled, but also hinge on the personal decisions of the scientist or on other extra-scientific circumstances.

Levins was the first to notice the existence of tradeoffs and the fact that scientists are compelled to choose a certain strategy, and he also put forth his own typology of these tradeoffs. The scientist can choose whatever desiderata should prevail in the model – either generality, or realism or precision, but never all three of them at once. There always have to be some virtues which are preferred and some that are neglected. Thus the scientist faces a trilemma and is pressed to adopt one of the following strategies: either sacrifice generality to realism and precision, or sacrifice realism to generality and precision, or sacrifice precision to realism and generality.

Over the time the theorist proposed other taxonomies of trade-offs. For example, Matthewson and Weisberg put forth a typology in which they identified three types of tradeoffs: “strict tradeoffs”, “increase tradeoffs”, and “Levins tradeoffs” (which drew on Levins’ original concept).³⁵ Unlike Levins, Matthewson and Weisberg maintain that generality, which features prominently in many theories of science as a desired theoretical virtue, comes in more than one kind. Thus, they distinguish among two types of

³³ There are also other issues that further complicate the situation – the model doesn’t count on perpetual genetic changes in population, etc.

³⁴ *Ibid.*, 422.

³⁵ John Matthewson and Michael Weisberg, “The Structure of Tradeoffs in Model Building,” *Synthese* 170, no. 1 (2009): 189.

generality within the models and propose a new concept of a relationship between these two types and precision.

In general, the majority of scientists admit the existence of at least some tradeoffs, although some theorists raised criticisms.³⁶

Which Factors Determine the Scientists' Decision?

The multiplicity of models of natural phenomena and the plurality of selection criteria demand an answer to the question of what the determinants in the selection process are. As suggested above, the non-availability of a generally accepted rational and formalized method for a model selection process suggests that there must be other factors at play. When factors such as the empirical characteristics of the modelled phenomena or its representational logic are not able to explain the selection, it is apparent that we must look for the answer somewhere else, and this is where the “subjective” or “external” factors enter the picture.

As we have seen in the first example of modelling at Loch Leven, external factors can be detected for example in the purpose of the scientific project, which was in this case an analysis of the impact of climate change and pollution on the Loch's ecosystem. In general the factors determining the final features of the model can be divided into several groups such as the background of the scientists and the research tradition they work in, the purpose of the modelling and finally the available technology and methods at their disposal.³⁷

³⁶ Orzack raised some critical issues for the concept of tradeoffs, which were later dispelled by Levins himself and other authors. Criticism of Levins' claims is given for example in Steven Hecht Orzack, “The Philosophy of Modelling or Does the Philosophy of Biology Have Any Use?” *Philosophical Transactions: Biological Sciences* 367, no. 1586 (2012): 170–80 and other articles. Other authors rebutted the criticism, e.g., Jay Odenbaugh, “Complex Systems, Trade-Offs, and Theoretical Population Biology: Richard Levin's ‘Strategy of Model Building in Population Biology’ Revisited,” *Philosophy of Science* 70, no. 5 (2002): 1496–507.

³⁷ This was the case of modelling the trout populations in Montana rivers as well. Taper maintains that the choice of one particular selection criterion over another depends also on the purpose of the modelling task, i.e., a scientist can apply one criterion for empirical models (where the goal is to minimize the prediction error), and another for mechanistic or descriptive models – and this is fully legitimate because these models serve different purposes. And selection criteria lead to varying results since they single out specific qualities of these models. (See Taper, “Model Identification from Many Candidates,” 494.)

Background of the Scientists

From historical studies of science (Fleck, Polanyi) it is clear that scientists do not live in a social vacuum, but that they form distinct groups and collectives with particular research traditions that impact upon the way in which they approach their work. After providing an affirmative answer to the existence of tradeoffs, Levins himself sought to uncover these unknown elements in decision making.³⁸ He asserts that the one of the factors that shapes decision-making is the background of the scientists. According to him, physicists entering the field of population biology conform to the tradition of their original discipline and tend to build models with general yet unrealistic equations and thus sacrifice realism to generality and precision. They seek idealized models typical in physics and do not take into account the fine details of the workings of a real-world ecosystem such as “time lags, physiological states, effect of a species’ population density on its own rate of increase”, because they expect that these effects will cancel each other out. In a similar vein, fishery scientists who work in the field take a more practical approach that requires precise and testable predictions and sacrifice generality to realism and precision. Levins, a farmer turned population geneticist and mathematical ecologist, found himself in the third group, together with a handful of other authors – they sacrifice precision to realism and generality, since they are more concerned with the qualitative rather than the quantitative features of the model. Thus each group resolves the trilemma by choosing other preferred virtues.

By the same token, Wangersky debunked how “social” factors such as the background of the scientists translated into their work and modelling itself. He hypothesizes that biology is occupied by two distinct groups – theorists and experimentalists, wherein the former often come from mathematics or physics and lack the necessary knowledge of biological principles, and the latter are “innocent” in mathematical techniques.³⁹ This tension results in different modelling philosophies or approaches, in which these groups tend to create models with diverse qualities such as generality or predictive power.

Aims of Modelling

We have seen that in addition to the background of the modelling, its aims also have implications for the choice and final form of the model. Several

³⁸ Levins, “The Strategy of Model Building in Population Biology,” 422–23.

³⁹ Wangersky, “Lotka-Volterra Population Models,” 189–218.

classifications of models based on their goals have been proposed – they take into account the different purposes of the models, or their distinctive features.

Taper, Staples, and Shepard⁴⁰ emphasized that scientists must take into account the scientific question that the model seeks to answer. The choice is often based on the model's "ability to answer questions of interest", which can depend on the purpose of the modelling – either theoretical or practical (applied science). As a result, the model selection method can vary. Based on their examination, they also pinpointed two pathways for developing models in biology: either to build exploratory complex models which however fit poorly to data and give unreliable predictions, or to build a host of simpler candidate models.

Wagnersky furnished yet another typology of models which plays on their quintessentially opposite approach as to how they grapple with natural phenomena and the aims of their construction.⁴¹ Models serve different purposes and that is why they do not look and perform the same. They can be distributed along a spectrum, where at one end would be the descriptive models and on the other end analytical models. Descriptive models aim to "condense" the empirical data, and they display a close fit to it. Analytical models, on the other hand, seek primarily to describe the mechanism of the system as they are mostly based in logic and lead to a better conceptual understanding of the system and its dynamics. Analytical models can boast of better predictions in unstable or changing conditions, whereas descriptive models perform better when the system is stable. Most models fall in between these two extremes.

State of Technology

Decision making necessarily involves other outside influences such as the state of technology and current methods employed by the scientific community. This can be illustrated in the changes brought about by the proliferation of computers in contemporary science, which has also been one of the driving forces behind the extensive use of models in science.

Other factors notwithstanding, computers play a decisive part in the model selection process. While the human researcher is prone to favor models that capture the essence of the studied phenomenon, computers

⁴⁰ Taper et al., "Model Structure Adequacy Analysis," 357–70.

⁴¹ Wagnersky, "Lotka-Volterra Population Models," 189–218.

do not possess such restrictions except for their own computational capacity. Without a doubt, computational limitations that plagued generations of scientists before the era of computers no longer have much relevance for present research. Complex biological systems can be successfully modeled not only in population biology but also in other disciplines such as genetics. This recent development has been strongly felt in modelling. Turney in his analysis of modelling practices argues that, since computers can now handle hundreds of variables, the decisions regarding the choice of models should be shifted from the dilemma of accuracy–simplicity as stated before to the dilemma of accuracy–economy (of computation) and thus reflect the potential of modern technology.⁴² In his view, in contemporary science, despite the massive computer power there is still an unsubstantiated tendency to favor simpler models, which cannot be explained by anything other than inherited routines and practices of the scientists.

Lastly, it is not only the power of hardware that makes its mark on the business of modelling, but also the choice of software that shapes the thinking of the scientists, as is a well-known occurrence not only in biology but also other disciplines that rely heavily on modelling (such as sociology or economics). In biology, Levins noted this trend already in the 60s and coined for it the pertinent term “Fortran ecology”, as Fortran was the dominant programming language used in biological modelling in his days.

As we have seen, the difficulties implicit in model building and selection cannot be fully ameliorated. It is obvious that scientists’ backgrounds and their research traditions, together with the purpose of the modelling and the available technology and possibly other factors are implicated in the way the problems are articulated and solved in modelling. These factors play an important part in model building and selection in biology and cannot be circumvented.

Conclusion

There is a necessary corollary to the fact that all models are abstract and simplified representations of phenomena: in the process of model building, a loss of information about the target system that is being modelled appears. This loss can appear in various stages of the modelling process. In addition, the extent to which we lose information from the target system is to some

⁴² Peter Turney, “The Curve Fitting Problem: A Solution,” *The British Journal for the Philosophy of Science* 41, no. 4 (1990): 511.

extent arbitrary, and can be minimized or maximized by the decisions made by the scientist. The result is the multiplicity of models in biology. On top of that, the criteria devised to help us balance out some of these conflicting demands also vary. All these factors have a bearing on the final form of the model. And, since there is no clear distinction between models and theories in biology, all these findings apply to biology theories as well. Henceforth, in our view, the legitimacy of the underdetermination thesis is established in the biological sciences.

This conclusion also has far-reaching implications for other tenets in the philosophy of science. For example, if we take a closer look at one of the scientific virtues, parsimony, which is the embodiment of Occam's famous medieval dictum "*Non sunt multiplicanda entia sine necessitate*": Occam's razor echoes prominently in most of modern science, and it is also – as we have seen – a fundamental principle in modelling. However, closer analysis reveals that it should be considered rather as a successful heuristic rule which doesn't have much of a scientific substantiation itself, since it was devised as a concession to the weakness of human minds. As some authors (Turney) claim, at present computers can handle more variables than ever, but in scientific practice there is still a significant preponderance of simpler models. Thus, parsimony as a principle is applied more for the convenience of humans – and this is exactly where internal representational logic and rationality of research clash with human limitations and values.

The inadequacy of the human mind was acknowledged already by Levins,⁴³ who deems that the existence of a plurality of models is inevitable, because of the irreconcilable conflict between the limited capacity of the human mind and the inherent richness and diversity of nature. The human mind is not able to embrace the heterogeneity of natural systems and because of this seeks to reduce complexity into simpler and comprehensible models, which is also an expression of the innate human search for understanding and control.⁴⁴ Odenbaugh, in his defense of Levins, provides similar argu-

⁴³ Levins, "The Strategy of Model Building in Population Biology," 431.

⁴⁴ In relation to this issue, yet another question begs to be answered: Besides the practical considerations such as the limitations of computational power, are there any inherent limits to modelling stemming from the fact models as well as theories can be understood as formal systems? There are indications that there is some substance to this idea. For example, Suppes, who claims that models in the empirical sciences, e.g., in physics, biology, and economics, can be recast as axiomatized formal systems (i.e., set-theoretical entities, which comprise a set of objects, relations and operations on these objects), also advanced the idea that there is no substantial difference between these models in the well-developed empirical sciences and those in pure mathematics, see Patrick Suppes, "A Comparison of the Meaning and Uses of

ments. He contends that the natural complexity of the world results in epistemological difficulties.⁴⁵ Scientists have only restricted cognitive abilities to handle the given load of information and operations involved in certain types of mathematical representations.⁴⁶

Occam's razor is just one of the many factors that intervene in model building. As I have shown, there are a number of other entwined factors – scientists' backgrounds, pressures of tradition, tacit research assumptions, purpose of the research, all of which effect to a various degree an imprint on the products of science, i.e., models and theories. If we accept their incursion into science, we come closer to the views propounded by sociologists or philosophers of science, who are credited (or criticized) for bringing a portion of “non-rationality” into science. Besides Kuhn or Feyerabend, who built their philosophies entirely around the extra-scientific or non-rational factors in science, it was among others Hesse⁴⁷ who broached the topic of “non-logical” or “extra-empirical” values with regard to models, or Bloor, whose Strong program strives to uncover the “social” considerations of scientific theories.⁴⁸ This view obviously stands in opposition to the convictions of some traditional hardline rationalists with their creed that science is always rational and that empirical data impose only one possible interpretation. The

Models in Mathematics and the Empirical Sciences,” *Synthese* 12, no. 2/3 (1960): 289, 294. But this approach, which conceives of models as formal systems, inevitably opens the door for all its ensuing mathematical, logical and philosophical implications. (A somewhat contradictory picture is painted e.g., van Fraassen, *Scientific Image*, 56). Van Benthem adhered to this line of thought and linked the foundational issues in mathematics such as axiomatization, derivability, definability, consistency, completeness, and decidability with theories in the empirical sciences and he sees these issues as relevant to theories in empirical sciences (Johan Van Benthem, “The Logical Study of Science,” *Synthese* 51, no. 3 (1982): 451–52). Yet, if this is the case, would then, for example, the limitations such as Gödel's incompleteness theorems apply to modelling too? Since empirical models (such as the examples cited in this article) make extensive use of mathematics applied to real-world phenomena, these constraints would apply. Although these hurdles might seem quite insignificant to current empirical sciences – for such purely formal models are seldom construed – they can, however, squelch enthusiasm for the ultimate prospects of mathematical models of nature. As van Benthem and Suppes realized, one of the prime examples – in which these concerns would not be merely hypothetical – is the debate about reductionism, which is seminal for all empirical sciences.

⁴⁵ Odenbaugh, “Complex Systems,” 1499–500.

⁴⁶ And he also adds that other pitfalls for the scientist-modeler stem from the chasm between the simplified and controlled environment at a scientist scientists' lab on the one side, and complex living nature on the other.

⁴⁷ Mary Hesse, *Revolutions and Reconstructions in the Philosophy of Science* (Brighton: Harvester Press, 1980).

⁴⁸ David Bloor, *Knowledge and Social Imagery* (Chicago: University of Chicago Press, 1991).

conflicting views of these two groups can hardly be reconciled. However, the position of the former and their perspectives seem to be *vis-à-vis* the evidence presented in this article vindicated.

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