# The Meaning of "Theory" in Biology

organized by Massimo Pigliucci, Kim StereIny, and Werner Callebaut

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Konrad Lorenz Institute for Evolution and Cognition Research Altenberg, Austria

### The topic

Our workshop deals with the meaning of "theory" in biology as seen from the different points of view of philosophers, theoretical biologists, and empirical scientists. Historically, philosophers have always been interested in how scientists formulate and deploy the theoretical concepts that both guide and are molded by empirical research (Lyons 2003). Evolutionary theory in particular has been the focus of attention ever since Popper's famous misunderstanding of it, followed by a less well known but significant recantation of his original views (Popper 1978). Today's philosophical analyses of evolution are better informed than Popper's and delve into much more scientific detail, to the point of often being indistinguishable from theoretical biology proper (Okasha 2005; Pigliucci and Kaplan 2006; Walsh 2007).

Scientists, on the other hand, have been generally rather disinterested in, and in some instances even downright contemptuous of, philosophical contributions to science, as in the case of physicist Steven Weinberg's essay, "Against Philosophy" (in Weinberg 1992). However, there have been exceptions, particularly among biologists interested in areas such as species concepts, phylogenetics, and the limits of evolutionary science in general (Lewontin 1963, 2000; Pigliucci 2003). This relatively small group of scientists keen on cross-talk with philosophers has managed to maintain a tenuous but consistent bridge between the two disciplines and modes of inquiry, particularly in the case of individuals like Richard Lewontin, who quickly came to be highly respected in both fields.

More recently, a small but increasing number of both philosophers and scientists have articulated or simply started to practice an approach that has been referred to as "the continuation of science by other means" (Chang 2004) or, informally, "sci-phi" (Pigliucci 2008). In this borderland between philosophy and science, scientists engage in conceptual meta-analyses that resemble philosophical work, while philosophers write papers that are close in nature to theoretical science papers. Moreover, an increasing number of scientists and philosophers have be-

gan to publish together not only in philosophy journals (a practice that has a long history in the field) but also in scientific ones (Pigliucci and Kaplan 2000; Laland et al. 2006; Glass and Hall 2008).

A further reflection of this trend toward the creation of a science-philosophy hybrid area of theoretical reflection is the creation of new journals devoted to it. A pioneer in this sense was *Biology and Philosophy* (currently edited by K. S.), which for years has offered a platform for dialogue between biologists and philosophers of science. More recently, the KLI has sponsored the publication of *Biological Theory: Integrating Development, Evolution, and Cognition* (edited by W. C.). And recently a third journal of this kind, *Philosophy* & *Theory in Biology* (co-edited by M. P.), has seen the light. And these outlets are just a part of a small but expanding publishing landscape that includes, for instance, forays in this area by publications such as *Acta Biotheoretica* and the *Quarterly Review of Biology*.

#### Aims of the Workshop

The workshop aims at gathering together a number of philosophers and biologists interested in the structure, foundations, and practice of biological theorizing in a broad range of fields, with an emphasis on organismal biology (ecology and evolutionary biology). We wish to explore topics that include but are not confined to the meaning and deployment of mathematical modeling in the biological sciences, the limits and potential of theoretical approaches and how they relate to empirical research, the social impact of biological theories, and the politics of theorizing in science. In some sense, this will be a follow-up to the 10th Altenberg Workshop in Theoretical Biology, "Modeling Biology: Structures, Behavior, Evolution," organized by Luciano da Fontoura Costa and Gerd B. Müller in 2004 (Laubichler and Müller 2007).

In particular, we will focus on the aforementioned theme of the development in the life sciences of the disciplinary hybrid of theoretical reflection. We will ask participants to consider whether theoretical reflection has a distinctive role, and why it has developed around the life sciences but not, for instance, geology. We will explicitly raise the question of whether "theory" means something different for the life sciences, and whether theory plays a role in biology that somehow contrasts with its role in other sciences.

Indeed, even within the life sciences, an argument can be made that there exists a marked contrast between evolutionary biology, which is structured around and unified by an overarching theory, and ecology or developmental biology, which at the moment—are not. What explains the fact that there is nothing comparable to the Modern Synthesis in these other areas of biology?

It is very clear that different kinds of activities count as "theoretical" in biology: on the one hand, one can take, say, population or quantitative genetic modeling as an example of standard theory based on mathematics. But inherently nonmathematical concepts such as Schwann's cell theory or, more recently, Eldredge and Gould's "punctuated equilibria" are also clearly theoretical and, arguably, have had an even larger impact on the actual practice of biology. Are these somehow completely distinct ways of doing theory? Is there a broader sense of the concept that encompasses both? These are some of the questions we will pose to the participants to the workshop.

The overall idea, of course, is not to turn philosophers into scientists, and much less to urge scientists to become philosophers. Rather, we begin with the acknowledgment that the two fields have independent histories and agendas that ought to be respected in their own right: broadly speaking, science's aim is not to replace philosophy (*pace* rather brush statements by scientists like E.O. Wilson); nor is it philosophy's goal to help science solve scientific problems (*contra* the aforementioned Weinberg). However, we also think that there is a suitable ground for reciprocal intellectual fertilization that can benefit from the different know-hows and intellectual approaches typical of scientists and philosophers.

Broadly speaking, then, we are after a better understanding of what it means to

do "theory" in science, and in particular in biology, although comparisons with how "theory" is understood in other sciences, particularly physics, will of course need to be part of the discussion. We suspect that philosophers will come to the workshop with perhaps a broader if less sharply defined understanding of theorizing than the scientists, and that even among the latter there will be significant differences between, for instance, mathematically oriented and empirically driven practitioners.

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# The Meaning of "Theory" in Biology

Thu 30 June	Evening	
6.00 pm		Welcome reception and dinner at the KLI

Fri 1 July	Morning	Introduction	Chair:
		Evolution and Ecology	Sterelny
9.30 am – 9.40 am		Announcements	
9.40 am – 10.25 am	Pigliucci	On the Different Ways of "Doing Theory" in Biology	
10.25 am – 10.50 am	Coffee		
10.50 am – 11.35 am	Millstein	Exploring the Status of Population Ger The Role of Ecology	netics:
11.35 am – 12:20 pm	Collins	Natural Selection and Ecological Theo	ry
12:20 pm – 2.00 pm	Lunch	at the KLI	

Fri 1 July	Afternoon	Some Current Hot Spots	Chair: Vorms
2.00 pm –2.45 pm	Cleland	Is a General Theory of Life Possible? the Origins and Nature of Life in the Co Single Example	Jnderstanding ontext of a
2.45 pm –3.30 pm	Bruggeman	Theory as a Guide in Molecular System	ns Biology
3.30 pm – 4:00 pm	Coffee		
4.00 pm – 4.45 pm	Leonelli	Classificatory Theory in Biology	
4.45 pm – 5:30 pm	Gross	Selective Ignorance and Multiple Scale Deciding on Criteria for Model Utility	es in Biology:
6.00 pm	Departure for Dinner	at the restaurant "Waldschenke" in the	Vienna Forest

Sat 2 July	Morning	Re/presentation of Theories	Chair: Roughgarden
9.00 am – 9.05 am		Announcements	
9.05 am – 9.50 am	Love	Theory Is as Theory Does	
9.50 am – 10.35 am	Vorms	Theorizing and Representational Practices in Classical Genetics	
10.35 am – 11.00 am	Coffee		
11.00 am – 11:45 pm	Hammerstein	Risking Deeper Integration: The Role of Theory in Biology	
11.45 am – 12:30 pm	Griesemer	A Model of Theories in the Inexact Sciences	
12.30 pm - 2.00 pm	Lunch	at the KLI	
Sat 2 July	Afternoon	Evolution of Cooperation Social Impact	Chair: Collins
2.00 pm –2.45 pm	Roughgarden	Theory in Trouble: The Evolution of So	ocial Behavior
2.45 pm –3.30 pm	StereIny	Co-operation in Complex Society	
3.30 pm – 4:00 pm	Coffee		
4:00 pm – 4:45 pm	Kaplan	From "Theory" to Social Impact and Back Again: Measures of Genetic Diversity and the Meanings of Race	
4.45 pm – 5:30 pm	Longino	Behavioral Sciences in the World	
6.00 pm	Departure for Dinner	at the restaurant "Mormat" in Vienna	

Sun 3 July	Morning	Beyond the "End of Theory" in Biology	Chair: Pigliucci
9.30 am – 9.35 am		Announcements	
9.35 am – 10.20 am	Depew	The Rhetoric of Evolutionary Theory	
10.20 am – 10.50 am	Coffee		
10.50 am – 11.35 am	Callebaut	Beyond a Theory of Biological Theorie	S
11.35 am – 12:20 pm	All	Participants' Discussion	
12:20 pm – 2.00 pm	Lunch	at the KLI	

#### Abstracts

Massimo PIGLIUCCI City University of New York

#### On the Different Ways of "Doing Theory" in Biology

"Theoretical biology" is a surprisingly heterogeneous field, partly because it encompasses "doing theory" across disciplines as diverse as molecular biology, systematics, ecology and evolutionary biology. Moreover, it is done in a variety of different ways, using anything from formal analytical models to computer simulations, from graphic representations to verbal arguments. In this essay I explore a number of aspects of what it means to do theoretical biology, and how they compare with the much more restricted sense of theory in the physical sciences. I also tackle a recent trend toward the presentation of all-encompassing theories in the biological sciences, from general theories of ecology to a recent attempt to provide a conceptual framework for the entire set of biological disciplines. Finally, I discuss the roles played by philosophers of science in criticizing and shaping biological theorizing. **ROBERTA MILLSTEIN** 

University of California Davis

#### Exploring the Status of Population Genetics: The Role of Ecology

The status of population genetics has become hotly debated among biologists and philosophers. Many seem to view population genetics as unchanged since the Modern Synthesis, and have argued that subjects such as development were left out of that synthesis. Some have called for an extended evolutionary synthesis (e.g., Massimo Pigliucci); others think that a more extensive remodeling is required (e.g., Lindsay Craig). Yet Michael Lynch, in a twist on Dobzhansky's famous slogan, has declared that "nothing in evolution makes sense except in the light of population genetics." Missing from this discussion is the use of population genetics to shed light on ecology and vice versa, beginning in the mid-1960s and continuing until the present day. Population genetics may not be required for all evolutionary explanations, and it may not incorporate all the causal factors of evolution, but it is a powerful tool that continues to be used and modified. JAMES COLLINS Arizona State University

#### **Natural Selection and Ecological Theory**

In 1986 the paper "Evolutionary ecology and the changing use of natural selection in ecological theory" appeared in the Journal of the History of Biology (JHB). The paper summarized an analysis I did showing that up until the mid-1960s it was common to find arguments in which population- and community-level traits were explained by the action of natural selection acting on populations or communities. The emergence of evolutionary ecology in the 1960s, and especially the publication of G. C. Williams's Adaptation and Natural Selection in 1966, virtually extinguished these claims. In particular, Williams argued that selection among genes or individuals could explain the evolution of most traits and therefore population-, community-, or ecosystem-level arguments were unnecessary. For some decades the issue seemed to be resolved. But 25 years after the publication of the JHB paper there is again a series of arguments that natural selection at the population or community levels does indeed have a place among the theoretical explanations for variation in population sizes and community traits. In this paper I will look at these changes over the last 25 years as a way to understand the relationship between theoretical approaches and how they relate to empirical research in biology.

CAROL E. CLELAND

University of Colorado

# Is a General Theory of Life Possible? Understanding the Origins and Nature of Life in the Context of a Single Example

The claim that universal biology is impossible because all distinctively biological generalizations describe highly contingent states of nature is currently very popular. Proponents of this view fail to appreciate, however, the degree to which our experience with life is limited. Despite its astonishing morphological diversity, all life on Earth is remarkably similar at the molecular and biochemical level; it is for this reason that biologists believe that all life on Earth shares a last universal common ancestor. Yet as I discuss, biochemists and molecular biologists have established that life could be at least modestly different in some of its basic molecular and biochemical characteristics, and they generally concede that no one knows just how different it could be. Indeed, it is possible that familiar Earth life provides not only a single but also an unrepresentative sample of life. In short, it is scientifically premature to draw much in the way of conclusions about the prospects for a universal theory of life.

This raises the question of what if anything can be inferred about life, considered generally, from our current scientific understanding of familiar Earth life? In addition to a greater emphasis on understanding prebiotic chemistry, I argue that more attention needs to be paid to the microbial world, which differs in structure, dynamics, and evolutionary mechanisms in underappreciated ways from that of large multicellular organisms. It is tempting of course to treat these differences as providing yet more grounds for despairing of a universal biology. But it seems clear that microbes represent the earliest forms of life and moreover are far more common in the universe than large multicellular organisms; indeed, the latter are fairly recent arrivals, having emerged on Earth less than a billion years ago, whereas there is compelling evidence that microbes date back at least to 3.9 billion years.

As I also discuss, one of the things standing in the way of universal biology is the continued grip on biological thought of the old Aristotelian paradigm for life, which (significantly) was founded upon studies of plants and animals. Aristotle's influence is clear in popular definitions of life as well as scientific theories of the origin of life; even Darwinian accounts owe a poorly acknowledged debt to certain facets of his work. An adequate understanding of the general nature of life—assuming that it has such a nature—almost certainly requires abandoning this framework. Indeed, it is perhaps telling that it was the abandonment of Aristotle's phase-dependent concept of material substance (in terms of four basic elements, water, air, earth, and fire) that played the critical role in the development of a universal theory of chemical substance.

#### FRANK BRUGGEMAN

Netherlands Institute for Systems Biology

#### Theory as a Guide in Molecular Systems Biology

Living cells are complex molecular systems that actively sense and adapt to environmental dynamics. This adaptive dynamics is an emergent property of vast molecular networks involving thousands of (macro)molecules. Mathematical modeling and theory are becoming increasingly important for cell biology to make sense out of experimental data. Molecular systems biology is a discipline that integrates methods from engineering, mathematics, and physics to explain how molecular mechanisms give rise to cellular behavior.

I will shortly review the current status of molecular systems biology and the role of theory. Integration of classical biological theories, such as population genetics, game theory, and ecology, with new theories about the dynamics, physics and control of molecular networks is the current challenge. This process will lead to the next generation of biological theories and mathematical models with a firm molecular basis. Those are anticipated to explain the emergence of life from the organism's genome and the dynamics and structure of its molecular networks. SABINA LEONELLI Egenis, University of Exeter

#### **Classificatory Theory in Biology**

Scientific classification has long been recognized as involving a specific style of reasoning and ways of doing research (e.g. by Ian Hacking and John Pickstone). In this chapter, I explore the characteristics of theories generated through classification activities in biology, which I refer to as "classificatory theories," with particular attention to the case of bio-ontologies recently used to classify genomic data for the purposes of dissemination and re-use. I argue that this type of theories, which emerges from classification practices in conjunction with knowledge of the materials and specific circumstances (lab set-up, field site) used for research, expresses the knowledge underpinning the analysis, interpretation and re-use of data.

## LOUIS J. GROSS National Institute for Mathematical and Biological Synthesis and University of Tennessee

# Selective Ignorance and Multiple Scales in Biology: Deciding on Criteria for Model Utility

Much of the scientific process involves "selective ignorance": we include certain aspects of the systems we are considering and ignore others. This is inherent in the models that we utilize as proxies for biological systems. Our goal usually is to isolate components of these systems and consider them at only certain temporal and spatial scales. The scales and questions induce different metrics for what might be considered a "good" model.

The study of mathematical and computational models is replete with differing views of the terms verification, validation, corroboration, etc. I have often argued that criteria for determination of model utility should be established prior to model construction, but this is rarely done in many areas of biology. The question I address is whether it is feasible to develop a general approach to model evaluation, that includes all the forms of models typically applied in biology—animal and cell/tissue culture ones as well as mathematicaland computational ones.

ALAN LOVE University of Minnesota

#### Theory Is as Theory Does...

Forrest Gump's recitation of his mother's proverb—stupid is as stupid does—is intended as a common sense reminder to characterize things in terms of their activities rather than their advertisements. In this paper I pursue a related theme with respect to the meaning of theory in biology. Recent philosophical discussions have stressed the difference between methodologies oriented toward scientific theory and those oriented toward scientific practice. But the practice of using theories (what theory does) can tell us something about the nature of theories (what theories are). I will concentrate on how evolutionary theory exhibits multiple structures that are displayed in the theory presentations utilized in biological practice. These partial representations can be characterized as idealizations that intentionally depart from features known to be present in the theory without presuming there is a single structure for it.

#### MARION VORMS

Institut d'Histoire et de Philosophie des Sciences et Techniques, Paris

#### **Theorizing and Representational Practices in Classical Genetics**

The goal of the paper is to challenge theory-biased approaches to scientific knowledge in biology, by showing the fruitfulness of a study of representational practices. I consider classical genetics, and I highlight the crucial role that was played by the invention and development of linkage mapping in the structuration of this theoretical domain in the 1910s and '20s. This representational technique embodies the articulation of two different theoretical frameworks, viz., cytology and Mendelism. I show that approaches focusing on laws, concepts, explanatory patterns, and even on "schemes of reasoning" (Kitcher 1984) miss important aspects of the articulation of these two theoretical frameworks, and tend to obscure the process theorizing as well as the very conceptual content of classical genetics. I argue that the construction, manipulation, and interpretation of concrete representations such as linkage maps are the very *locus* of *theorizing*, rather than a way to express (and access) an underlying abstract *theory*.

#### PETER HAMMERSTEIN

Humboldt-Universität zu Berlin

#### **Risking Deeper Integration: The Role of Theory in Biology**

In my view, the four elements of theoretical biology are (1) data analysis and representation, (2) mathematical model building, (3) concept formation, and (4) integration of knowledge and approaches. Bioinformatics, for example, gives us tools for data analysis and representation that serve as the "virtual microscope" of the 21st century. Evolutionary biology, on the other hand, helps us understand the design of organisms through mathematical models that capture the selective forces responsible for this design. All mathematical efforts would be useless, however, where they not guided by concepts, such as information, memory, adaptation, regulation, feedback, robustness, modularity, etc. We use these concepts in different fields of biology and observe that different biological systems are faced with the same fundamental problems. To illustrate this point, consider the immune system and the extremely different nervous system. These systems are capable of learning and have found their own ways of doing it. They both share a major problem, however, in that they have to cope with the so-called stability-plasticity dilemma. It is the power of abstraction to reveal such a similarity and thus to counter the centrifugal forces fragmenting the life sciences. This is where theoretical biology may play its most important role.

JAMES GRIESEMER

University of California Davis

#### A Model of Theories in the Inexact Sciences

Model-based views of scientific theories take theories to be, or to be presented by, a family of models. But there are two routes to theory specification or presentation implicit in such views: one based on theoretical investigation and one grounded in empirical inquiry. These two routes to models, from theoretical vs. empirical inquiry, have different implications for the relation between a scientific theory and phenomena in its empirical domain and how that relation figures in pursuing the various aims of science: description, understanding, explanation, prediction, or control of nature.

In this essay, I consider how these implications might be traced by distinguishing exact from inexact science. For a science to be exact, its theory must be formalized. I characterize formalization broadly-more broadly than simply expression in quantitative terms—as any distinction of form from content in the phenomena to be represented in order to provide scope for exact sciences that are not "mathematical" in the most familiar senses. In exact sciences, theory (plus formalization principles and investigator goals) determines whether a structure constitutes a model of the theory. In inexact sciences, empirical practice (plus representational strategies plus investigator goals) rather than formalized theory determines whether a structure constitutes a model for the theory. The status, character, and role of models differ in the two kinds of sciences in part because of these two different routes of model building. I discuss examples of exact and inexact biological sciences, specialties and lines of work in order to reveal varying roles and modes of modeling and formalization practices. JOAN ROUGHGARDEN Stanford University

#### Theory in Trouble: The Evolution of Social Behavior

The now classical picture of social evolution from the 1960 and '70s relied on the hypotheses of kin selection, group selection, and reciprocal altruism to explain the evolution of altruism (and cooperation), and on the hypotheses of competition for mates with good genes followed by parental conflict of interest to explain the evolution of family organization. This picture has been dissolving in light of continuing empirical and theoretical discoveries. New approaches to the evolution of cooperation and family life are offered by Nash bargaining theory for modeling biological "teamwork," and by the notion of biological "firms" for producing off-spring. The reluctance of present-day biologists to confront inconvenient data, and their vigorous policing of dissident views, point to widespread ossification in the theoretical framework for understanding social evolution and jeopardize the future of behavioral ecology.

#### KIM STERELNY

Australian National University and Victoria University of Wellington

#### **Co-operation in Complex Society**

This paper will revisit well-known themes in evolutionary thinking: the role of models, Mayr's proximate-ultimate distinction, and Tinbergen's related "four questions" in the explanation of behavior. It will do so through the lens of explanations of human cooperation; in particular, cooperation in the evolutionary transitions between egalitarian and complex society. I shall suggest that to understand this transition, we need to understand the interrelations between evolution-ary and proximate mechanisms.

#### JONATHAN KAPLAN

Oregon State University

## From "Theory" to Social Impact and Back Again: Measures of Genetic Diversity and the Meanings of Race

While the results of scientific research often have direct impacts upon society, the theoretical underpinnings of that research are only rarely implicated in influencing social policy decision making. The results of contemporary biological research have had profound impacts upon society, in arenas spanning almost every technical domain (pharmaceutical development and production, medicine, agriculture, chemical production more generally, etc.). But aspects of biological theory have had profound impacts upon society as well—perhaps not always as obvious or direct, but important nonetheless.

In this paper, the relationship between some aspects of biological theory and social policy will be explored in the context of the theoretical justifications for particular approaches to measuring genetic diversity (both within and between populations) and the uses of these approaches to address questions regarding the biological reality and/or importance of human "races." Misunderstandings surrounding the different measures of genetic diversity and their relationship to intuitive understandings of diversity have fueled confusion regarding what kinds of technical results are evidence for what kinds of broader claims; understanding the conceptual limitations of the technical results is an important first step to-wards ameliorating that confusion. HELEN LONGINO Stanford University

#### **Behavioral Sciences in the World**

This talk reports on an investigation of the differential uptake in media of different levels of sophistication of work representing different approaches to the scientific study of human behavior. The approaches include both quantitative behavioral genetics and molecular behavior genetics, developmental psychology, neurophysiology and anatomy, as well as a number of integrative approaches. The media range from professional journals to middle-brow lay publications. Implications for understanding the impact of scientific research on social matters are considered.

### DAVID DEPEW University of Iowa

#### The Rhetoric of Evolutionary Theory

I discuss whether rhetoric of science offers a useful supplement, corrective, or challenge to philosophy of science, and specifically to philosophy of evolutionary biology. To do so I offer remarks about the three terms (1) rhetoric, (2) theory, and (3) evolution.

(1) I set aside as unhelpful definitions of rhetoric as tropological window dressing and as expressive insight after the manner of Goethe, Humboldt—and the young Darwin. I treat rhetoric as addressed argumentation within the context of controversies.

(2) I take scientific theories to be identified not by the mathematical formalisms they apply, but by the conceptual frameworks or ontologies (*sensu* Carnap and Quine) that apply and interpret these formalisms. I claim that in the heat of controversies theories whose frameworks apply persuasively to some topics are, when carried on the wings of these frameworks far beyond the scene of controversy, as empty (and ideologically contaminated) as Kant says the categories are when extended beyond the "bounds of sense." Rhetoric as situated argumentation illuminates this process in ways that compensate for philosophy's bias toward universal applicability and nomic necessity, but complement the so-called semantic view of theories.

(3) Evolutionary biology shows this dialectic more clearly than other natural sciences, including functional biology, because it deals with historical particulars that make for good cases but limited generalizations. I argue that rhetoric of evolutionary biology so conceived, rather than inducing skepticism and relativism, protects the epistemic claims of evolutionary biology in ways that philosophy of science has not always managed to do.

#### WERNER CALLEBAUT

KLI and Department of Theoretical Biology, University of Vienna

#### **Beyond a Theory of Biological Theories**

Although "theory" has been the prevalent unit of analysis in the philosophy of science for a long time, the concept itself remains remarkably elusive (Gorelick 2011). On the hypothetico-deductive (HD) view, a theory may be understood as "offering hypotheses from which, in combination with empirical assumptions, deductions can be made regarding empirical results" (Lloyd 1988). But, as we now know, the merits of HD accounts of science-Popperian or other-are modest, to put it mildly, and probably hopeless in the case of biology. On the non-statement (or structuralist, or semantic, or model-theoretic) view as applied to biology by Lloyd, Thompson, Krohs, and others, theories are extra-linguistic entities that may be characterized by a number of different linguistic formulations. On one influential reading, they are "collections of models and their robust consequences" (Griesemer 2002, after Richard Levins). The non-statement view is one among several post-positivist developments in the philosophy of science that enable "sciphi" accounts (Pigliucci 2008) to stay much closer to actual scientific practice than the traditional "rational reconstructions" by philosophers. It also suggests that a monolithic account of "theory" is not to be had.

In this paper, I try to get a handle on *what theories do for scientists—biologists in particular*—by (1) revisiting some old dichotomies such as theory vs. evidence and theory vs. practice, (2) comparing hybrid ("sci-phi") meta-analyses and meta-syntheses in biology with their counterparts in the social sciences, in particular economics, and (3) reflecting on corrolary notions such as explanation, prediction, understanding, organization of existing data (Colyvan 2011), perspectives and images (Griesemer), hypothesis- and question-driven research (Glass and Hall 2008), and theory as "vision" (Woese). In doing so I will also (4) pay attention to *the changing roles of theory in biology* since the mid-19th century.