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THEMATIC ISSUE ARTICLE: THE MEANING OF ''THEORY'' IN BIOLOGY

Formalization and the Meaning of "Theory" in the Inexact Biological Sciences

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Abstract Exact sciences are described as sciences whose theories are formalized. These are contrasted to inexact sciences, whose theories are not formalized. Formalization is described as a broader category than mathematization, involving any form/content distinction allowing forms, e.g., as represented in theoretical models, to be studied independently of the empirical content of a subject-matter domain. Exactness is a practice depending on the use of theories to control subject-matter domains and to align theoretical with empirical models and not merely a state of a science. Inexact biological sciences tolerate a degree of "mismatch" between theoretical and empirical models and concepts. Three illustrations from biological sciences are discussed in which formalization is achieved by various means: Mendelism, Weismannism, and Darwinism. Frege's idea of a "conceptual notation" is used to further characterize the notion of a form/content distinction.

Keywords Darwin · Exact and inexact science · Formalization · Mendel, model · Theory · Weismann

> I do not want to give the impression that the application of models in the empirical sciences is mainly restricted to problems which interest philosophers of science. Suppes (1960, p. 296)

> …it is not the real world which the exact sciences are capable of treating with an arbitrary exactness, but their own model systems. Gánti (2003, p. 55)

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Theory in Exact and Inexact Sciences

One meaning of theory in the inexact biological sciences is that theories of such sciences are not "mathematical" or "mathematized." Mathematized scientific theories are ones for which the principles, axioms, or propositions of the theory are presented in mathematical form. Since mathematics is often understood as, or as akin to, an exact science, the use of mathematics to specify or represent a scientific theory is one way to interpret a science as "exact." Sciences that have, or involve, informal theories could be construed as inexact sciences. Thus, non-mathematical (or as yet un-mathematized) biological sciences are inexact sciences.

Many philosophers and scientists first think of algebraic equations representing state changes of natural phenomena over time when they think of examples of mathematized scientific theories, such as Newtonian mechanics or population genetics. Further, philosophers of science might imagine that mathematization of theories is a goal of developing sciences. It would be too narrow a view of mathematics and science, however, to suppose that all empirical sciences either are exact or aspire to be so. Descriptive and comparative embryology, anatomy, and alpha taxonomy (description and naming of biological species) are all inexact sciences in this sense since none of them has a mathematical theory, and they may not have mathematization of theories as a goal, yet each is principled and governed by rules of procedure. In the case of taxonomy, the rules are explicit and established by international conventions such as the international codes of zoological and botanical nomenclature.[1]

[1] For the ICZN, see http://www.nhm.ac.uk/hosted-sites/iczn/code/. For the ICBN, see http://ibot.sav.sk/icbn/main.htm. Consulted July 20, 2012.

Indeed, the centuries-old contrast between natural history and natural philosophy might be construed as a contrast between inexact and exact sciences. If one takes natural history to be as scientific as natural philosophy, then the descendants of natural history are candidate inexact sciences. Some interpreters might argue that D'Arcy Thompson (2000) had mathematized descriptive anatomy, yet one may still question whether his mathematical approach to biological description counts as a *theory* of anatomy.[2] One might also argue that numerical taxonomy has a quantitative method, but not a mathematical theory. On the other hand, some (Eldredge and Cracraft 1980) have argued that phylogenetics is about sets (of taxa) and set theory is a branch of mathematics. At the very least, systematics has become a quantitative science (Hull 1988; Hagen 2003). Suppes (1960, 1962, 1967), in promoting a semantic conception of scientific theories, argued that sciences should be interpreted in terms of the mathematical (e.g., set-theoretical) rather than meta-mathematical (syntactic-logical) structure of their models. He also argued that "model" has the same meaning but different uses in the empirical sciences and mathematics (see also van Fraassen 1980, Chap. 3). Suppes' argument (1960, p. 293) suggests that the interplay of uses—of models as material or non-linguistic objects (of study) and models as realizers of a formal theory—matters to philosophical understanding of empirical science.

In exploring the meaning of theory in the inexact biological sciences, I will focus on the interplay of uses of models and meanings of theory in formalization practices. Even a cursory survey of these practices across just the biological sciences, however, is beyond the scope of this essay. Instead I will briefly discuss three disparate examples to illustrate the abstract points. One problem that arises, in general, in this interplay is divergence between the structure of empirical models redeployed in the specification or construction of theories as collections of models, and the structure of theoretical models as possible realizations in the representation of theories (conceived as propositions or sentences). Because collections of models used to construct a theory from an empirical base need not be identical with collections of models used to represent a theory logically, there can be significant "mismatches" between the models produced in the practice of empirical sciences and those considered by philosophers to be adequate formal representations of scientific theories.

My argument has three parts. First: on a theory-centric conception of exactness, I argue that mathematization is sufficient but not necessary for formalization (unless an extremely broad conception of mathematics is adopted). A science is not exact because its theory is mathematized but because: (1) its theory is formalized, and (2) its formalized theory is used to precisely control its subject domain and to align its theoretical models (possible realizations of theories) with empirical models of phenomena (representations of possible realizations of phenomena) by subject-matter appropriate choice of idealizations and abstractions. Thus, a theory can be formalized, yet its use fail to control the subject domain or align models and hence the science remains inexact. I understand phenomena to be the results of interactions of investigators with "nature." The resultant phenomena can serve as subject matter in particular domains of scientific practice and theory. Empirical models represent phenomena (in certain respects and degrees), while theoretical models are objects that satisfy specified (formal) theories. By "control" I mean determination and delimitation of the empirical content proper to the theory, just as a score defines a work of music, "marking off the performances that belong to the work from those that do not" (Goodman 1976, p. 128). By "alignment," I mean matching or coordinating the structure of models whose uses are directly empirical with those whose uses are directly theoretical.[3]

Second, on the narrower construal of exactness of a science as due to the mathematical formalization of its theory, a non-mathematical theory in an inexact science can nevertheless control its subject domain to a degree. Formal theories delimit proper empirical content, while informal theories can only incompletely and imprecisely circumscribe content. Mathematical population genetics theory is, precisely, about those structures that satisfy it. Moreover, theoretical models used to specify theories formalize them, while empirical models can be used for this purpose only indirectly and informally. Mendel's empirically derived "laws" of genetic transmission are more properly a model of an empirical phenomenon, but he was unsure whether they could be used to specify the theory he intended, since his Hieracium experiments didn't comport with the laws as his Pisum experiments had (Nogler 2006).

Alignment of theoretical and empirical models can be fairly unimportant to inexact sciences that are in the process of constructing a theory, since such sciences are open

[2] Compare Gould's interpretation of Thompson as a theorist in his foreword to the (1992) Cambridge edition with Bonner's more ambivalent introduction to the same edition. The former calls Thompson's work a contribution to theoretical biology while the latter states that Thompson "was quite satisfied with a mathematical *description* or a physical *analogy*" (Thompson 2000, p. xv, emphasis added).

[3] A use is indirect if it is a change of use or "repurposing" from another. My belt buckle has a direct use in holding up my trousers, but an indirect use as a bottle opener because it happens that its structure is suited to that function as well, and I sometimes repurpose my belt buckle while traveling if I've forgotten my Swiss Army knife, which carries my regular bottle opener.

as to what the full set of principles or propositions of the theory is or should be. It would be inappropriate to constrain empirical modeling by requiring alignment with theoretical models of a theory under construction. Most inexact sciences operate with loose collections of partially specified, partially understood, theoretical propositions or principles rather than with otherwise already specified or formalized theories. In these inexact sciences, a degree of "mismatch" between theoretical and empirical models that "mediate" between theory and phenomena is tolerated, but the general idea is that the mediation of theory/phenomena relations by models requires consideration of two kinds or roles for models: empirical and theoretical.[4] Inexact sciences may either be practices in search of a theory or practices that get on quite well without one, thank you very much. Differently put, there is less pressure in the inexact sciences (out of concerns for consistency, completeness, universality, or truth) for alignment of theoretical models that (semantically) specify the theory in question with empirical models that represent data. Mismatch suggests that a theory must fail to adequately explain or predict phenomena, yet mismatched theoretical "structures" can serve as effective conceptual, computational, and empirical guides because the resources to control the subject-matter domain come from elsewhere than formalized theory.[5]

On my view of formalization, to be theoretical, a model must not only be structured so as to realize or satisfy an intended theory, but also used in particular ways, including domain control and guidance of alignment processes. In the practice of inexact sciences, empirical models occupy center stage—they are all the representations one needs in order to fulfill the functions of theory such as explanation, organization, interpretation, and prediction of phenomena, as well as heuristic guidance of further empirical inquiry.[6] In exact sciences, theoretical models occupy center stage—they are the theory presentations[7] that serve both to specify the theory and serve as the realizations of which the theory is true exactly. This difference in use resolves pragmatically some of the logical problems posed by critics of semantic or syntactic views of theories.[8]

Part three of the argument is that some biological sciences might be viewed as having become exact once their theories were mathematized. Examples include theories of inheritance, ecology, systematics, and evolution, which have all gained mathematical "components," "cores," or "frameworks" in the twentieth century. Many textbooks, for example, present these theories in terms of their mathematical cores—consider theories of transmission, population and quantitative genetics (e.g., Bulmer 1985; Gillespie 2004), population ecology (e.g., Hastings 1997), phylogenetic systematics (e.g., Felsenstein 2004), and neo-Darwinian evolution (again see Gillespie or Hastings).

This is an extremely theory-centric way of characterizing the history of a science, however. One might consider other sources of inexactness in the history and practice of a science—in measurement, experiment, or observation, for example. It is conceivable that a science could have a mathematized theory but count as an inexact science if the latter are characterized in terms of "modes" of inexactness and informality besides in their theories.

[4] On the mediating role of models, see Morgan and Morrison (1999).

[5] "Match" is used here to avoid more specific connotations of correspondence, isomorphism, or even similarity. I prefer the imagery of alignment, as in making railroad tracks laid from the west and from the east align in the middle so that trains can run smoothly in either direction. Alignment of models is like that: the aim is to connect phenomena and concepts smoothly. As Winsberg (2006, 2010) has argued, when models of different domains don't align, scientists are willing to engage in various ad hoc "handshaking" arrangements to keep the trains running anyway. I think his points apply to models within domains of inexact sciences as well.

[6] Characterization of theory in terms of what theory does, materially, in relation to empirical content, has been emphasized recently by Love (2008 and 2012, this issue) and Brigandt (2010).

[7] On theory presentation, see van Fraassen (1980, p. 44); see also Griesemer (1984), and further discussion and elaboration in Love (2012, this issue).

[8] On challenges to the semantic view, see e.g. Morrison (2007, 2011); for a defense of the semantic view, see Thompson (2007). Critics make the compelling point that mismatch in the exact sciences appears to undermine the semantic view of theories. The exact sciences control their subject-matter domains precisely by means of formalized theories that delimit what count as proper subjects. The truth of formalized theories of a domain controlled by them is all too easy, since an object can belong to the domain only if it satisfies the theory. Hence Giere (1988; Giere et al. 2006) describes the role of theory as one of *definition* of a class of models. The problem arises for the semantic conception that scientific theories are intended to be true of their *empirical* subject matter as well, yet empirical contents of phenomena are related to models by relations of idealization and abstraction that, strictly speaking, render them *false* (Wimsatt 1987). On the semantic view, the theoretical models that precisely satisfy theories in the logical, Tarskian sense of model theory, cannot also be *correct* representations of empirical phenomena because empirical models must idealize and abstract from the phenomena in order to be useful representations. Empirical models, moreover, are often explicitly and intentionally false (i.e., partial, inaccurate) descriptions of phenomena, and often the models of a collection are intentionally designed to contradict one another as part of a research program to discover robust theorems (Levins 1966; Wimsatt 1987, 2007). Thus, if theoretical models satisfy theories and at the same time are expected to be idealized, false descriptions of empirical phenomena, even the best theories would have to aim at being both true and untrue of the empirical phenomena that the models describe. On the "twilight" of the perfect model model of science as aiming at exact natural laws that truly represent nature, see Teller (2001).

Population genetics might be characterized as an inexact science with an exact or formalized theory, if we take its theory to be mathematically formalized, yet note that empirical study of population-genetic phenomena involves measurement and experiment on phenotype distributions involving *presuppositions* regarding the causes—e.g., molecular genes, particular environments—of those phenotypes. On the other hand, one might recognize genotype/phenotype mapping relations as a part of a mathematical theory (Wagner 2010), and thus, just more mathematization (e.g., Thompson 2007). The notion that a science is exact if and only if its theory is mathematized is vague to the extent that it is vague what mathematics is. If population genetics inference involves "inexact," even if quantitative, measurement of (hypothetical) genotypes and environments in terms of (empirical) phenotypes, then the science would be inexact on the broader notion that a science is inexact if it involves any mode of inexactness in its practice. Allowing that a mathematized statistical theory of experimental design, hypothesis testing, or confirmation confers exactness on an empirical practice, perhaps one could then consider the science of population genetics exact, since both theory and practice could be considered mathematized.

Characterizing exact sciences in terms of formalized theories and formalization as mathematization yields a rather narrow base of concepts with which to analyze the wide diversity of biological sciences. Even narrower characterizations might specify the particular variety of mathematics (or logic) involved, such as specification of a theory in terms of set theory or linear algebra or first-order predicate logic with identity. A broader, but still theory-centric characterization of exact science might be that an exact science has a "formalized" theory, construing "mathematization" as a particular form of formalization. What might drive a choice of breadth of characterization? What is the best choice of a relation of formalization to "exactness" of theory? And what relation of theory to targets of empirical investigation best explains scientific practices?

These are big questions that have occupied the philosophy of science for over a century and philosophers in general for two millenia. In the following sections, I aim to do two much more modest things than to answer them: (1) take a broad stance on formalization, so as to gather a wide variety of biological sciences, practices, and theories; and (2) characterize exactness in terms of roles for theorizing in the practices of empirical biological sciences, in order to characterize theory in the inexact biological sciences. I suggest progress can be made on the big questions by considering borderline cases of formalization as well as central exemplars among the narrow group of widely acknowledged, exact, mathematical biosciences. I also suggest that more attention to scientific practices in the production and use of formalization can lead to a more interesting view than one that assumes all formalization is "mathematization."[9]

The abstract arguments above were not focused on analyzing any particular inexact science in detail. While I adopted a theory-centric perspective for the sake of argument, I do not endorse theory-centrism as an adequate approach to understanding any empirical science. Instead, my aim is to push theory-centrism toward the practice pole of the theory/practice dichotomy. Nor do I endorse the dichotomy as an adequate approach to philosophy of science: I never met a dichotomy I could trust. Rather than trust the dichotomy, my larger goal is to undermine it by considering a wider range of theories and theoretical practices than those that inspire easy comparisons to mathematical physics, such as population genetics and population ecology. In my view, "theory-ing" is a species of practice.[10] The question is: what are the roles of theorying in scientific practice? In developing a characterization of theory in the inexact biological sciences, I endorse a pragmatic rather than semantic or syntactic conception of scientific theories (Griesemer 2000). It is not my goal to argue that a pragmatic view of theories is superior to these other views or shares nothing with them, but rather to illustrate the value of a pragmatic view and emphasize that choice of a view of theories is a form of philosophical modeling of science. I will not address whether the views developed here apply beyond the biological sciences.

Philosophers have tended to introduce formal methods from logic, such as specifying a theory axiomatically, set-theoretically, or model-theoretically, because philosophers understand and value those tools and virtues. But the fact that a theory formalized in first-order predicate logic with identity cannot be both complete and consistent has never been the show-stopper in empirical science that it was for mathematics when Gödel proved it in 1931 for arithmetic (see Nagel and Newman 1958). The practice of theoretical science cannot be stopped by semantic or even syntactic "flaws" by the lights of a particular philosophical framework of formalization, but a theory, true or false, that is no use to scientists is a dead theory, full stop. These points suggest that a pragmatic view of theories is needed to explain theory-ing in practice.

A pragmatic conception of the concepts I have been discussing will help frame illustrations drawn from several inexact sciences: Mendelism, Weismannism, and Darwinism. I leave open to what extent each of these sciences has

[9] Perini (2004), for example, argues that visual representations can bear truth, hence diagrams can function as theoretical models in the senses explored here.

[10] I resist the implication of the term "theorizing" of a one-way path from phenomena to theories—turning something that is not theory into something that is. I do not presuppose that is the only or even the primary path of "theory-ing."

become (more) exact due to formalization of core theories. Formalization can be broadly characterized as drawing a form/content distinction so as to make possible the study of form independent of content. In order to draw such a distinction, certain forms and contents must be identified and delimited, so formalization in this broad sense can serve the function of subject-matter domain control. At the same time, a distinction of form and content facilitates two routes to theory construction: one from empirical contents toward the specification of theoretical forms, and one from theoretical forms toward satisfaction in empirical contents.

Exactness of a science can be understood as degree of conformity to a social convention to abide by a set of rules of application so as to render a set of theoretical principles or propositions constitutive, complete, and "relevant." Differently put, exactness is a form of discipline. To be an exact science, the principles or propositions of a theory must be taken to be well-formed formulas, primitives, grounds for inference, axioms. (There are many ways to characterize commitments to forms and conformity with rules.) Often empirical success in abiding by theoretical conventions requires "rigging" experiences, e.g., studying phenomena generated in the controlled conditions of a laboratory rather than in the wild.

Specification is a concept attributed above to the construction and identification of theory in terms of theoretical models, but theory also plays a role in specifying/guiding the empirical practices that form the basis for generating new theoretical models. Theory specification supports characterization of the forms of phenomena to which one can/should attend and which contents the forms apply to, and not only by providing resources for explaining, describing, interpreting, and predicting phenomena (see Love 2012, this issue).

In the next section, I briefly illustrate three formalization "moves" in inexact sciences: Mendelian genetics, Weismannian cyto-embryology, and Darwinian evolution. These are steps taken in empirical work that lead to formalization and the use of formalized principles to align theoretical and empirical models (or, one might say with van Fraassen, embed empirical models or substructures in theoretical models) and to guide empirical practice. These are, according to my view of formalization, steps also necessary to take a collection of theoretical models to be models of a theory. Whether they fulfill the requirements of model theory, as possible realizations or satisfiers of a theory, remains open in these cases, because I focus on inexact sciences or sciences which were inexact at the historical moment of these formalization "moves." Each "move" involves the establishment of a conceptual notation through which a form/content distinction is made. The notation can be used to represent empirical data and also serve as (or to build) theoretical models that specify a formal theory. The formal theory can be used to align theoretical and empirical models (e.g., by showing how to embed the latter in the former) and also to guide further empirical practice (e.g., by drawing attention to novel structures, relations, or, in general, forms whose instantiations can be tracked empirically, or by making predictions about novel observations or experiments that might be made).

Formalization in Three Inexact Biological Sciences

Mendel's Factor/Character Distinction and the Emergence of an Exact Science of Genetic Transmission

Mendel (1866) said his theory is a theory of "development from the hybrids," which he generated by tracing crosses of purebred lines of pea plants (Griesemer 2007). The challenge in formulating a principle to explain this development was that Mendel found that there are two kinds of constancy in the development from hybrids: constancy of form and constancy of behavior. Can one principle explain both? In modern terms, constancy of form results from the activity of homozygotes while constancy of behavior results from the activity of heterozygotes. Heterozygotes generate the same array of forms in which their parents appeared while homozygotes generate the same forms among offspring that they themselves have. The modern description of Mendel's work relies on a form/content distinction Mendel drew in the course of developing a conceptual notation in his paper that affords tracking of factors (*Anlagen*) in terms of characters (*Merkmalen*). This factor/character distinction is a kind of form/content distinction. Differences between Mendel's notation and modern genetic notation reflect further formalization of the theory of classical transmission genetics.

One bit of evidence for the view that Mendel sought a single principle to account for both kinds of constancy is that he used his conceptual notation to expand symbolic expressions representing progeny of a cross by grouping symbols according to the kind and degree of constancy, rather than by grouping terms that emerge from systematic mathematical cross-multiplication of terms of the binomial expansion. His two-factor crosses, resulting in approximate 9:3:3:1 ratios, grouped terms that are constant in form in both characters (AB + Ab + aB + ab), then those terms constant in form for one character and constant in behavior for the other character (2ABb + 2aBb + 2AaB + 2Aab), and then the term for constancy in behavior in both characters (4AaBb), viz.: AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb. In writing the terms this way, I suggest that Mendel was trying to understand the developmental relation between the two kinds of constancy by distinguishing the empirical content or character state of plants from the formal determinants or "factors" determining frequencies of contents in crosses of a given structure, so as to reflect that relation in his expansion of mathematical terms.

The essence of Mendel's theory (identified by Bateson's footnote in his translation of Mendel's paper) is informal and qualitative: a principle of like combining with like or unlike.

> So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilising pollen are of like character. We must therefore regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in one plant, or even in one flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells, as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms. (Mendel 1965, p. 20)

That is Mendel's theory as Mendel expressed it (Griesemer 2007). There is nothing about random assortment of gametes in that theory. It is a theory about development from hybrid forms of characters. The formalizing move in the presentation of Mendel's theory (in what modern genetics takes to be Mendel's "laws") occurs when Mendel adds a probabilistic assumption that facilitates the mathematization of the informally combinatorial theory. This additional assumption, together with the development and use of a conceptual notation marking a distinction between factors and characters, are the first steps toward formalizing a theory of the development of pure and hybrid plants–plants developed from like or unlike parents. He calls the additional assumption a hypothesis, which I propose to read as a hypothesis that his theory of development can be successfully formalized if the assumption is made. Mendel writes:

> In point of fact it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations, *if we might at the same time assume* that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers." (Mendel 1965, p. 21; emphasis added)

The equal *numbers* assumption (added to Mendel's equal *sorts* theory quoted previously) starts as an inference from the empirical data on the pure forms and then is extended, by hypothesis, to cover the hybrid forms as well. Purity and hybridity are "tracked" according to the conceptual notation developed in the paper, but the formalization afforded by this theoretical hypothesis of equal numbers allows the theory to be used to align the resulting theoretical model ("Mendel's laws") with the empirical models of data that Mendel describes earlier in the paper. The alignment is worked out by a proof of the equivalence of several different notations that Mendel uses to describe the data and what would follow from the theory together with the equal numbers hypothesis (see Griesemer 2007 for details).

Moreover, the alignment and formalization of the theory facilitates prediction from the theoretical model in backcrosses that have a different structure than the ones the empirical models were designed to represent, i.e., a cross between an offspring of a hybrid to one of the parental types that produced the hybrid progeny. Because the theoretical model extends to the behavior of the pure forms among the progeny of hybrids, it can guide further empirical practice in ways the empirical model of crosses producing constant progeny cannot. The probabilistic equal numbers assumption makes the conceptual notation into a probabilistic, combinatorial theoretical model "sufficient" to describe the constancy of form of the pure types and constancy of behavior of the hybrids. The "backcross" experiments show the power of the conceptual notation and the success of the formalized theory in guiding prediction and explanation of new phenomena.

More importantly for understanding the role of the formalized theory in creating an exact science, the formalized theory creates a kind of "closure effect" on the subject-matter domain. The Kuhnian normal scientific activity of using Mendel's formalized theory to guide experimental practice, as articulated and amended in the emergence of classical transmission genetics, closes the domain of "Mendelian phenomena." Phenomena that do not behave according to formalized Mendelian theory are simply "non-Mendelian" phenomena. Failure of data to conform to the theory are problematic data, not (immediately) falsifications of the theory. As Gánti says (see epigraph), what the exact sciences are capable of treating with arbitrary exactness is their own model systems. The exact science of classical transmission genetics was initiated by Mendel in the formalizing moves I described. The addition of the equal numbers assumption to the informal theory, expressed using the conceptual notation, is a formalizing move because it allows one to say, on the basis of the specified theory rather than on the basis of exemplary empirical phenomena, what constitutes satisfaction of the theory by a model. The move also allows one to say what can count as an empirical substructure of that model which, given suitable idealizations and abstractions, bears the right relation to data so as to count as evidence supporting the empirical adequacy of the theory.

The formalizing move marks a shift from empirical modeling of phenomena and the search for theoretical principles to a theoretical framework "embodying" a completed set of principles that scientists can commit to in order to use the framework as a guide for model construction and alignment as well as production and tracking of new phenomena with new observations or experiments. The subsequent history of "Mendelian genetics" introduced new empirical models to deal with apparent inconstancy of form or behavior (e.g., anomalous ratios), which led to modification of the formal theory (e.g., to accommodate linkage and recombination), but from Mendel's formalizing work onward, it has always been clear that the theory dictates what constitutes a "Mendelian system." This conventional or definitional character of the role of theory in exact science comports well with Giere's (1988, 2006) account of the semantic view of theories. My account, however, emphasizes the pragmatic character of the *importance* of formalization of theory in the historical production of exact science; mathematizing the theory does not suffice to render transmission genetics exact. Delimitation of the domain by conventional use of the theory is also required.

Weismann's Germ/Soma Distinction and the Visual Formalization of Heredity-Development

Diagrammatic representation and diagram abstraction offer a contrasting mode of conceptual notation and formalization to the sort of combinatorial symbol system Mendel used to construct a formal algebra of hereditary transmission. Weismann and other "cell lineage workers" (Maienschein 1978; Griesemer 2007) made diagrammatic models of embryos developing in time by abstracting away spatial properties of cells observed in their camera lucida microscope setups (Griesemer and Wimsatt 1989). From drawings that represent the observational data, these diagrammatic abstractions left only cell genealogies and cell-type identities represented in systems of nodes and arrows. Weismann's fundamental distinction of germ and soma among the cell types that emerge in embryogenesis yielded a distinction of genealogical form—the pattern of cell lineage relationships—from embryological content—the specific nature of each of the cells of the developing body (Griesemer 2007). Used as maps for further empirical exploration, these diagrams served the emerging fields of cytology and genetics as guides, amplifying attention to certain sorts of phenomena that could be made to elicit their form and providing a theoretical structure in which particular representations of empirical data could be embedded.

Mendel's approach to formalization involved adding an assumption to an empirical model to make it mathematizable in such a way that the theory could be used to guide new empirical investigation in the form of predictions of data outcomes, e.g., of backcross experiments. With Weismann diagrams, a change in use of diagrams from models representing empirical phenomena to theoretical models specifying a theory became the basis for formalizing a theory that tracked cell fate along the lines of a distinction of genealogical form from cellular content in the representation of embryological phenomena. Formalization redirects the use of modeling from the goal of representing empirical phenomena directly toward the very different purpose of providing a guide or expectation of the structure, function, and behavior of units of analysis theoretically identified by the conceptual notation. These theoretical units can be used to guide empirical investigation via the formation of hypotheses (about the behavior of empirical systems), predictions about the data outcomes of observations or experiments, control policies and protocols for the regulation and production of desired effects, and explanations of empirical phenomena in theoretical terms.

The emergence of diagrams of Weismannism from cell-lineage work in the nineteenth century by Whitman, Boveri, Wilson, Weismann, and others is an example of formalization by visual means (Griesemer and Wimsatt 1989; Griesemer 2007; Wimsatt and Griesemer 2007). In cell-lineage work, embryologists moved from organ- and tissue-level study of developing embryos to consider cell-level differentiation under the microscope (Maienschein 1978). The history of this work can be represented visually, in a series of images beginning with "portraits" of embryos with diagrammatic elements (arrows) superimposed to illustrate the phenomenon of cell lineage. Cells of a developing multi-cellular embryo give rise to other particular cells (as the embryo grows by cell growth and division), differentiate into various body cell types, and go through morphogenetic movements which generate tissue- and organ-level organization (Fig. 1). In both the diagrams that track embryo development and in the history of the science, embryo pictures give way to cell-lineage diagrams, which increasingly abstract the "genealogical structure" or form of lineage relationships among cells from the "embryological content" of those cells, i.e., the shapes, sizes, spatial, and temporal relations of cells and distribution of distinctive materials within each cell, which together constitute the differentiated states of cells of different types in the embryonic body.

The culmination of this historical sequence of images appears in E. B. Wilson's textbook, *The Cell in Development and Inheritance* (1896), which became the canonical representation of "Weismannism" (Griesemer and Wimsatt 1989), represented in our era in developmental biology texts as recently as Gilbert (1985). The visual separation of genealogical form from cellular content formalizes the description of embryonic differentiation, repurposing the diagram from representation of data to theoretical model of

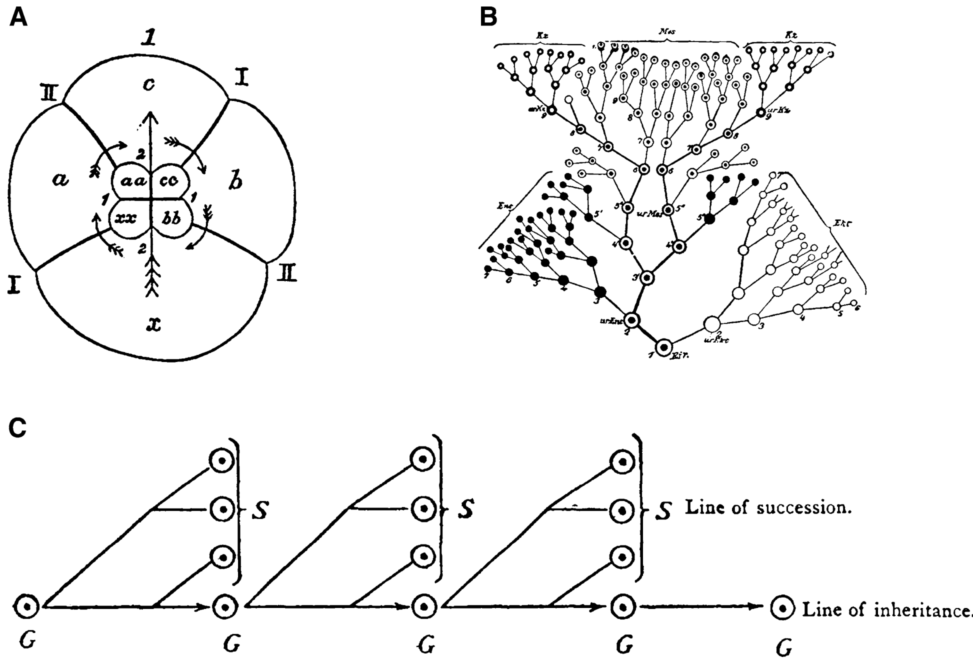

Fig. 1 Cell lineage diagrams. **a** a "semi-diagram" portraying early cell divisions of a freshwater leech from Whitman (1887, diagram 1, p. 109), **b** a cell lineage map of the germ-track of a worm by Weismann (1893, Fig. 16, p. 196) and **c** a "germ/soma" diagram by Wilson (1896). The diagrams display the distinction of genealogical form (cell lineage or genealogy) and embryological content (cellular identity, differentiation state, or fate) in increasingly abstract terms. See the text and also Griesemer and Wimsatt (1989) and Griesemer (2007) for discussion

a formal theory of "Weismannism." The theoretical structure can guide work in cyto-embryology and emerging theories of genetics and evolution in ways similar to what Mendel's formalized theory of hereditary transmission did for an exact science of transmission genetics. However, the rules and conventions for reading Weismann diagrams are not as explicit as those for manipulating algebraic symbols or working with probabilities. The structure of Weismannist theory is more open and thus its guidance, alignment, and domain control prospects may be more limited.

Frege's (1882a, b) arguments for the perspicuity of a two-dimensional conceptual notation for logic, in contrast to Boole's one-dimensional notation, led him to a diagrammatic method of separating logical form from mathematical content that visually resembles those of the contemporary cell lineage workers. Frege separated logical form, represented by a system of strokes, from mathematical content: thoughts, facts, and assertions. He argued that his notation was superior to Boole's, which mixed together logical and mathematical meanings of symbols for operations that could be used to represent logical form or mathematical content, but both together only in a confused way (Fig. 2). The perspicuity of a notation that affords separate attention to the logic and the mathematics, Frege hoped, would help put both on firmer foundations and, in particular, permit a formalization of logic as a subject distinguishable from mathematics. This was crucial to his foundational project to interpret mathematics in terms of logic.[11]

[11] Frege's logicism is usually contrasted with the psychologism of Boole and other nineteenth century logicians. If psychologism is a

The formalized theory tracing genealogical lineages of cells went unnamed until the emergence of transmission genetics and the theory of the gene following the work of Mendel in the early twentieth century. Whether a diagram functions as an empirical model of data or a theoretical model of a formalized theory depends on use. If this kind of diagram directs how to look for genealogical structures in nature (whether among cells, molecules, or species), then it is functioning as a formalized theory delimiting Weismannian developmental systems. Theoretical guidance can take the form of hypotheses (about the behavior of empirical systems in terms of a model), predictions about the data outcomes of observations or experiments, control policies for the regulation and production of desired effects, and explanations of empirical phenomena in theoretical terms.

Footnote 11 continued
form of "naturalism" about the subject domain of mathematics, Frege's logicist program looks to be anti-naturalistic about mathematics and, in my extension of his use of conceptual notation to the idea of formalization in the natural sciences, anti-naturalistic about science. A Fregean (in my sense), however, can be pragmatic about conceptual notation (perspicuity is a pragmatic virtue) while logicist about theory (in Frege's case, about the logical theory of mathematics). Thus, Frege can be opposed to psychologism in mathematics and an anti-naturalist about mathematics and at the same time, pragmatic in his practice of logic. (Everyone is pragmatic about their own practice, even if logicists and reductionists deny pragmatism to everyone else in their practices!) So, one must distinguish the pragmatic role of an effective notation for logic from the role (logicist or otherwise) of theory about a subject-matter domain. Conceptual notations are means of formalizing theory and thus facilitators of formalism about theory, yet one's stance on theory can be autonomous from one's stance on notation.

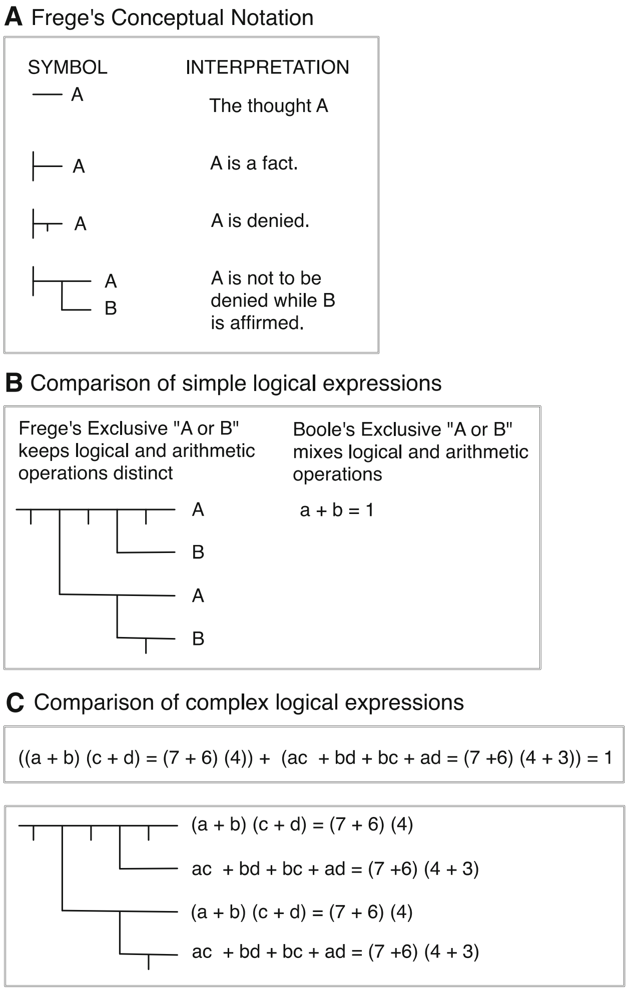

Fig. 2 Comparison of Frege's and Boole's notations for logical analysis of mathematical expressions. Frege argued that his two-dimensional notation was more perspicuous for complex expressions where it becomes paramount to distinguish symbols expressing logical form and symbols expressing mathematical content. See text for discussion

In early twentieth-century genetics texts, e.g., Walter (1913), the Weismannist theoretical model was aligned with empirical Mendelian models by showing that the behavior of Mendelian factors satisfied the formal Weismannist structure. Later in the twentieth century, Maynard Smith (e.g., 1965) argued that the structure of Weismannism's model is isomorphic to that of Crick's central dogma of molecular genetics: once genetic information gets into protein, it can't get out again. In Maynard Smith's argument, alignment of cyto-embryological and genetic models is also a means of domain control: flow of molecular information within a cell counts as genetic because its structure is isomorphic to the genealogy of the germ-line identified in Weismannism's model (see Griesemer and Wimsatt 1989).

In the twentieth century, the visually formalized theory of Weismannian developmental systems was also used by some to delimit what count as evolutionary systems, such as Richard Dawkins' (1982), p. 164) analysis of neo-Darwinism in terms of replicators and replicator theory as "fairly describable as 'extreme Weismannism.'" The Weismannist framework also provided the context for important critiques of "neo-Darwinism." Leo Buss's *The Evolution of Individuality* (1987) questioned the Weismannist assumption (and therefore a key formalizing move of early neo-Darwinism) when he pointed out that the Weismannian separation of germ and soma is really rather rare in nature, i.e., quite limited in phylogenetic distribution. Much recent debate about "major transitions" in evolution (e.g., Maynard Smith and Szathmáry 1995; Godfrey-Smith 2009; Calcott and Sterelny 2011) explores the character of various empirical phenomena that might better serve in the formalization of a generalized evolutionary theory than the cyto-embryological visualization of a germ/soma distinction.

In this too brief discussion, I have suggested that a diagram can serve the functions of a conceptual notation. In the case of Weismannism, however, the theory is formalized but not mathematized (unless diagrams of this kind count as a branch of mathematics, which graph theorists might claim). Much of twentieth-century biology came to focus more on documenting the wide variety of molecular and cellular mechanisms operating within the Weismannian framework than on producing a general mathematical "theory" of germ/soma relations, so the desire to align grand theoretical models with models of more direct empirical utility has perhaps been less imperative.[12] Indeed, as the molecular mechanisms known to affect heredity have proliferated and seem ever less unified, one might argue that heredity theory is becoming more informal rather than less by piling informal epigenetic principles on top of formal genetic theory.[13]

Darwin's Principles: Formalization by Extraction

Space does not permit developing the point in detail, but a third mode of formalization, besides overt mathematization of an informal theory (Mendelism) or diagram abstraction (Weismannism), is the extraction of "Darwin's Principles" from the body of Darwin's work (Darwin 1859) and elevation to the status of axioms.

[12] For an attempt to relate models of mechanism to theories, see Griesemer (2011a, b) and Love (2012, this issue).

[13] Love (2012, this issue) considers attempts to retain population genetics as a formal core of an exact science in the face of EvoDevo complications. Theoretical geneticists have also become interested in attempting to bring epigenetics under the umbrella of formal population genetics—e.g. Slatkin (2009); cf. Tal et al. (2010).

Lewontin (1970, p. 1) expressed Darwin's principles as a numbered list:

> As seen by present-day evolutionists, Darwin's scheme embodies three principles:
>
> 1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).
> 2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
> 3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable).
>
> These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change.

Lewontin's characterization is a third kind of example of what I mean by formalization. His presentation of Darwin's theory is neither a mathematization by means of an added assumption, as in Mendelism, nor a visualization by means of diagram abstraction, as in Weismannism. Lewontin's representation generalizes Darwin's theory by interpreting "individual" to mean a sort of variable ranging over "levels of biological organization" rather than restricting the theory's objects to organisms. Individuals comprising populations at any level in the compositional hierarchy from molecules to groups of organisms to whole species that satisfy the formalized principles can potentially be units of selection (see Wimsatt 1980; Lloyd 1994; Brandon 1990). The generalization establishes a distinction between the conceptual form of Darwin's theory as a theory applying to (biological) individuals and the empirical content Darwin mostly dealt with: organisms, but occasionally groups. The status and meaning of concepts of heredity, variability, and fitness are entangled in Darwin's work with the particular empirical qualities of mostly macroscopic, mostly multicellular organisms.

Darwin's own expressions of his "principle of natural selection" in *On the Origin of Species* are various. As a philosopher, I have tended to gravitate toward one in particular, on p. 61 of the 1st edition, because this is the version that most resembles Lewontin's formalization. But I think that is a mistake (as my colleague Roberta Millstein is fond of reminding me). It focuses attention on the theory formalized in terms of these generalized individuals to the exclusion of other versions and uses to which Darwin's theory can be put. It is not clear from either Lewontin on page 1 or Darwin on page 61 where to put Darwin's ideas about competition in and among populations, division of biological labor, the principle of divergence, the idea that natural selection has been the main but not exclusive means of modification, the principle of sexual selection, or the principle of use inheritance, in relation to the three principles that Lewontin extracted. Which principles—the Lewontin three or the expanded set just given—constitute the formalized Darwinian theory that should be used to delimit the domain of Darwinian evolutionary units or class of Darwinian evolutionary systems?[14] There is considerable controversy about what precisely Darwin's theory is, and hence what constitutes an adequate formalization. Lewontin gave us one, but it is not the only one. It is worth remembering that Darwin began experimenting with these principles as long ago as 1838 in his E Notebook on transmutation. Darwin's statement at E58 doesn't really look to me like Lewontin's version, though I grant that one is tempted by Lewontin's formalization to read that structure back into Darwin's 1838 version. There are lots of ways, for example, to interpret Darwin's third principle in the E notebook: "Great fertility in proportion to support of parents" besides reading it as "fitness."

Conclusion: Three Dimensions of an Informal Account of Formalization

Three key dimensions of formalization were identified in the foregoing examples: conceptual notation, model alignment, and subject-matter domain control. "Conceptual notation" is a form of presentation of the empirical contents of investigative experience,[15] which in a very broad sense is: (1) the production of a form/content distinction in the description and representation of scientist-"nature" interactions that produce phenomena; and (2) a (possibly tacit) convention (set of rules) governing or relating forms in the representations (models). "Alignment" reconciles representations (models) of forms and contents by coordinating the different kinds of models mediating between investigative experience and theory. This coordination involves structuring and interpreting models and theories in the hierarchy Suppes describes (1962, p. 259) so that the idealizations of ceteris paribus conditions, experimental designs, models of data, models of experiments (or other investigative interactions of scientists with subjects/"nature"), and theoretical models do not undercut their service as "possible realizations"—the

[14] See also Godfrey-Smith (2009) for a similar formalization around the idea of "Darwinian population."

[15] "Investigative experience" is intended as a generalization of Suppes' (1960, 1962) notion of "experimental experience," allowing for a distinction between observation and experiment on the one hand, and experimental and theoretical investigations as empirical experiences on the other. For an "investigative practice" approach to science, see Waters (2008).

hallmark of what Suppes calls the "logical conception" of models.

Thompson (2007) generalized insights of the semantic conception to all mathematical formalizations rather than only the set-theoretical predicate approach of Suppes and the state-space approach of Beth, van Fraassen, and Lloyd. He called this expanded semantic conception the "Galilean" conception in honor of Galileo's well-known view that the book of nature is written in the language of mathematics. I opt for a still broader, practice-oriented conception of formalization, one that outruns notions of the mathematical realm traditionally considered in most discussions of biological theories. "Mathematization" is the production of particular sorts of form/content distinctions in the specification of a theory by means of the construction or adoption of what Frege (1879, 1882a, b) called a "conceptual notation." Hence, I call my further expansion of the semantic conception, "Fregean."[16] I note that the Fregean conception is a greater departure from the semantic conception than Thompson's Galilean conception because the former is really a pragmatic rather than semantic conception of theories, which takes as fundamental the role of theories in practice or use, formalized by means of a conceptual notation, in the functions of domain control, model alignment, and guidance of empirical work.

A theory does not count as formalized unless its presentation in a conceptual notation is actually used in these practices. In other words, formalization is a practice, not merely a state, property, or condition of a theory. Successful formalization affords increased facility or even makes possible new kinds of theoretical and empirical practice unavailable without formalization. A distinctive kind of theoretical practice is made possible through formalization: investigative practices that have as their subject matter the forms (models) themselves and comparisons among them (cf. Suppes 1962, p. 261) rather than contents of empirical investigative practices (phenomena resulting from observations or experiments). Although examination and comparison of theoretical principles—such as Darwin's principle of natural selection and Malthus' principle of population, or Mendel's and Galton's (1876) principles of inheritance—is possible without formalization, the theoretical practice of investigating forms of order represented in empirical contents is at least greatly facilitated by formalization because of gains in perspicuity due to the use of conceptual notations. Mendel's notation (and those of his successors) is as important in facilitating new kinds of theoretical practice as their organization of empirical investigation had been in reshaping its domain of phenomena.

Additionally, theory-guided empirical practices are afforded by formalization. These are investigative practices that have as their subject matter the empirical contents that are indicated by the forms represented in models. This guidance stems from the role theoretical models can play in structuring the empirical activities and even attention and awareness of aspects of phenomena while investigators are empirically engaged. Although Darwin certainly was in the grip of certain creationist ideas along with a changing panoply of geological ideas during his Beagle voyage, once he had found "a theory by which to work," his attention to the "data" of variation in his field notes and observational reports could be systematically reexamined and fresh empirical studies guided by emerging principles.

Domain control concerns how the domain of investigation is established and its borders policed—i.e., what counts as a phenomenon in the domain. In exact sciences, theory controls the domain exactly while in inexact sciences similarity, historical precedent, patterns of interest and patronage, and empirical models control the domain.[17] Discovery of non-Mendelian inheritance, e.g., via epigenetic mechanisms, has not brought the theory of population genetics to its knees. Rather, the phenomena are labeled "non-Mendelian" and thus placed outside the proper domain of the given theory; some theoreticians then take up the challenge of this placement outside the domain and attempt to develop new theories (e.g., Tal et al. 2010) or else try to redescribe the exiled phenomena in terms that bring the traditional theory to bear and thus assimilate the new phenomena to the familiar domain (e.g., Slatkin 2009).[18] Attempts to regiment population ecology on a par with the exact science of population genetics usually meets resistance from a spectrum of ecologists, suggesting ecologists' allegiance lies more with the phenomena than with formal theory than seems to be the case with many population geneticists. This, of course, is a very crude sketch of a very weak contrast; exceptions abound. There are mathematical ecologists who delimit their subject matter in theoretical terms and there are evolutionary biologists who take the biological species concept as definitional or even metaphysical—treating all other species concepts as absurd or trivial. Phenomena that don't "fit" theory are ignored as someone else's problem rather than anomalies that must somehow drive a change in the formal theory.

These remarks about practice echo some of Kuhn's (1970) on the nature of normal, paradigm-governed science but with a twist. In the exact sciences, exemplars are nicely aligned with

[16] On notational systems in general, see Goodman (1976, Chap. 4).

[17] Phenomena deemed similar enough to phenomena already in the domain are also counted as in the domain. Phenomena investigated because they result as products of prior investigations are also counted as in the domain. Phenomena that fit empirical models developed to describe other phenomena are counted as in the domain. This is not to say that exact sciences escape the politics of historical tradition, interest and patronage, but the locus shifts at least partially to theory and theory-ing from empirical practice.

[18] Thanks to Massimo Pigliucci for this last reference.

the theoretical models that specify the central theory of a paradigm, but in the inexact sciences, normal science may not need a formalized theory if practice can be well guided without domain control. Other informal sciences I have studied suggest other means of domain control. Joseph Grinnell, director of the Museum of Vertebrate Zoology at Berkeley, partially delimited the domain of his studies (more or less) institutionally (Griesemer 1990). His was a California museum, so he took his domain to be the geographical borders of the state. No theory told him what phenomena to pay attention to. As his interest was in evolution "on the ground, as it happened," and his boots, horses, trains, money, and patron would only carry him so far, he didn't need a theory to specify what counted as a legitimate object of study. That said, Grinnell was a great theoretician working in an inexact science.

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