

## Material Models in Biology

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### 1. Introduction

Propositions are no more constitutive of science than they are of any activity: a body of knowledge is not all there is to the life of science. Thus I take the premise underlying the topic of this symposium to be uncontroversial, there *is* a “non-propositional” side of science and of biology in particular. From time to time, however, philosophers ask whether the “non-propositional” side of science is theoretically superfluous, or as Duhem put it, logically dispensable. What they mean to ask is whether science can be fully *analyzed* in propositional terms; must philosophy of science, in other words, consider the non-propositional side in order to adequately account for science?

Negative answers to the question often rest on the tacit view that the most (or only) *important* thing about science is scientific theories. Positive answers that are nevertheless framed in terms of theories usually take for granted the existence and function of “non-propositional” elements like non-literal uses of language (metaphors and analogies), diagrams, and pictures and try to show why they are irreducible to propositional content. What seems surprisingly uncommon is any attempt to search for systematic connections between the two as they function in science. There is of course a substantial literature on metaphor and analogy in science (e.g., Hesse 1966, Achinstein 1968, Leatherdale 1974), but this literature deals primarily with the role of figurative language in *contrast* to literal language rather than seeking systematic connections between the propositional and non-propositional contents of science.

In this paper I explore the boundary between the propositional and non-propositional sides of biological science, drawing on three cases with which I am familiar. It is important to stress that I focus only on the boundary between two perspectives on scientific *theory*, as exemplified by biological theories. I do not aim to address the larger questions of the non-propositional character of scientific practice *tout court*. I propose a picture of material model-building in biology in which manipulated systems of material objects function as theoretical models. Sometimes material models serve as direct theoretical models, as in non-mathematized fields of biology where structure may be abstracted directly from the material system without detour through

a formal sentential apparatus. Sometimes material models serve as vicarious, or indirect, theoretical models. That is, work with material systems can serve as an important basis for manipulation in thought of abstract, formal objects for the purpose of articulating a theory.

It is irrelevant to my analysis whether theoretical modeling, in so far as it yields scientific models with empirical content, is essentially or ineliminably vicarious. I do think the analysis is generalizable beyond the cases I discuss. In fact, I think there is very little in science that is ineliminable *ceteris paribus*. Vicarious theoretical modeling is certainly more common in biology in particular and science in general than philosophers realize, and as such it is a phenomenon in need of explanation. My aim is to describe an interesting and important feature of biological practice, not to show that it is essential to biological science.

My story is thus in contrast to Ruse's (this volume), which concentrates on Sewall Wright's illustration of mathematical ideas, already formalized, in his adaptive landscape pictures. It is also in contrast to Taylor's (this volume), in its reconstructive use of diagrams as a tool with which scientists are invited to represent their research field during an interview. My topic accords best with those aspects of Wimsatt's discussion (this volume) of the generative role of diagrams in biology. (Ruse and Taylor do discuss the generative, and hence non-superfluous, role of diagrams, but their cases are different because they consider non-propositional elements of science which are consequent on (presumably) propositional forms.)

In each of the cases I will discuss, material systems play important generative as well as presentational roles. In the first case (Grinnell's remnant models of faunas), a material system stands in for propositions and functions as a material "theory" in lieu of a propositional system formulated in natural language or mathematical equations. In the second case (Wright's path analysis), diagrams serve as a way to express causal hypotheses for the sake of generating precise mathematical propositions which can be tested. In the third case (Weismannism), diagrams serve as abstractions of causal processes in a background theory for the sake of generalizing a theory in the foreground of biological concern (Darwinian evolutionary theory).

I wish to illustrate an important point about the non-propositional side of biology by means of each of these cases: (1) material models are able to serve certain sorts of theoretical functions *more* easily than abstract formal ones in virtue of their material link to the phenomena under scientific investigation. "Remnant models," i.e. material models made from parts of the objects of interest, are of this sort. They are robust to some changes of theoretical perspective because they are literally embodiments of phenomena. If these embodiments are preserved, they may be studied again and again under different perspectives. This stability in itself depends on the creation of certain scientific institutions for the sake of remnant preservation and these institutional forms may thus serve as indicators for the presence of the models in scientific research.

(2) Diagrams can function as statement-generators if a set of rules for "reading" them is adopted as part of a theoretical methodology. In such cases it can be argued that this possibility makes formalized sentences themselves subject to the argument of eliminability that a traditionalist would apply to diagrams, metaphors and other structures resistant to the axe of first order logic. Thus diagrams can serve to facilitate theory-construction, possibly even supplanting more traditional modes of mathematical modeling.

(3) Diagrams can also hinder theory-construction in virtue of their representational power: they can become so entrenched in our way of theorizing that they outlive their theoretical usefulness. In serving to represent causal theories which function heuristically in the background of a given theory of interest, diagrams may provide strong ontological constraints on the way the foreground theory is understood. This may be true even if theory has advanced beyond the framework specified in the diagram simply because diagrams are powerful modes of representation that may become entrenched. Ruse makes this point, in rare agreement with Provine, in his paper on adaptive landscapes: Wright's diagram was constructed as a vast simplification of a mathematical theory within one theoretical framework describing the evolution of gene combinations, and then shifted to another framework describing the evolution of sets of semi-isolated populations for which the adaptive landscape diagram appears inadequate in its details. But despite its many inadequacies, Wright's diagram lived on in all its particulars among a broad range of evolutionary biologists. While the landscape diagram was obviously heuristically fruitful in its early use, it may be an obstacle to further work.

## 2. Grinnell's Remnant Models of Faunas

My first case concerns specimen collecting for ecological study in the Museum of Vertebrate Zoology of the University of California, Berkeley (MVZ). Joseph Grinnell (1877-1939), the MVZ's first director, was a Darwinian naturalist interested in questions of the geography of speciation and the character of the ecological environment (see Griesemer 1990). He is noted primarily for two accomplishments: an early formulation of the niche concept and for founding the MVZ. Grinnell became convinced that California was an ideal place to study evolution in an ecological context because compared to the east coast, the Pacific states were relatively unspoiled.

Grinnell, along with his patron-collector Annie Alexander, anticipated that the settling of California and the conversion of its economy to large scale agriculture would cause dramatic change in the higher vertebrate fauna of the state. They founded the MVZ in part to make a record of vertebrate diversity as it was known at the turn of the century (Star and Griesemer 1989). This prediction also presented an opportunity for research: Grinnell thought that Darwin's evolutionary theory needed expansion to include a description of the evolution of the environment, because that was what drove the force of Darwinian natural selection. If the vertebrate fauna could be studied continuously from the founding of the MVZ in 1908 for one hundred years, say, then evolutionary change caused by habitat and micro-climatic alterations could be studied in real time: California could be used as an ecological-evolutionary laboratory. In a well-known 1924 paper, Grinnell summed up his perspective:

Observation of species in the wild convinces me that the existence and persistence of species is vitally bound up with environments. The extent and persistence of a given kind of environment bear intimately upon the fate of the species we find occupying that environment. Environments are forever changing — slowly in units of recent time, perhaps. Yet with relative rapidity they circulate about over the surface of the earth, and the species occupying them are thrust or pushed about, herded as it were, hither and thither. If a given environment be changed suddenly its more specialized occupants disappear — species become extinct (Grinnell 1924, p. 153 in 1943 reprint).

The notion that ecological factors cause species to be herded into certain biological relations with other species and thus set conditions for Darwinian adaptation led Grinnell to classify environments in terms of ecological causes drawn from his expe-

rience as a biogeographer in the 19th century tradition of Wallace and Merriam. World realms, regions, life-zones, faunas, associations and niches comprised a hierarchy which could be used to classify the causes of the presence and absence of particular species or subspecies in a given location. Each level in the hierarchy was associated with a specific primary causal factor. Following Merriam, Grinnell thought of life-zones as defined in terms of physiological limits of temperature tolerance (e.g., Merriam 1894). Grinnell defined faunas primarily in terms of humidity, associations by local presence of plants that vertebrates might use for food, shelter or breeding sites, niches by the presence of constellations of other animal species to which the species in question was adapted to live.

Presence or absence of a taxon in a given place and time, along with information about the environment at that point thus constituted the basic data with which Grinnell would attempt to build a theory of the evolution of environment. Data gathered in particular field studies were typically summarized in maps indicating zones of homogeneity with respect to a given ecological factor; the most famous of these are the well-known "life-zone maps" (see, e.g., the life-zone map of California reprinted in Grinnell 1943). By studying shifting patterns in such data over time, Grinnell hoped to identify the significant causes and patterns of natural selection shaping species ranges and thus how their joint presence led to forces of organic adaptation. Fine-grained study of the distribution of subspecies would lead to an understanding of speciation (see Griesemer 1990 for a detailed account of Grinnell's argument).

We can conceptualize Grinnell's work on these subjects in terms of two notions: a remnant model of an ecological structure and an institutional specification for a vicarious program of theoretical model-building. The elemental structures that interested Grinnell were of the most mundane sort, the presence or absence of a given taxon in a location at a time. A list of taxon presences together with ecological information at a time can be taken to be a simple formal ecological model of that place and time. Alternatively, the specimens of those taxa with identifying tags linking them to a place, a taxon, and a set of environmental data, can be taken as the model of presences in a place at a time (i.e. an empirical substructure, see van Fraassen 1980). A theory of ecological change could be specified by assembling a collection of such models for different times and assigning ecological causes by classifying them according to their specific place in the ecological hierarchy.

The latter, material characterization of these simple ecological models has special significance. During the period Grinnell worked, there was great controversy in systematics over the proper characterization of species, in particular whether subspecies should be recognized as "real". Grinnell's models are what I called above remnant models. An environment is modeled by the organisms that occur in it and which are preserved as specimens along with information about ecological factors recorded in field notes by the collectors. Because the specimens are components of the model and ecological data recorded in notebooks can be keyed to specimens by labels, *models* can be preserved in a museum. This is significant because changes of theoretical perspective about the nature of species can be taken into account by pulling the specimens back out of their drawers or off the shelves and reanalyzing the model in terms of a different set of taxonomic designations. This is not possible in the isomorphic *formal* model because once the *information* is recorded that members of a particular taxon were present in a location, there is no recourse—through that information alone—to revise the assessment of specieshood that underlies it, should the theoretical perspective on the nature of species change. Only consultation with the original specimens will do. Even the collection of new specimens is insufficient because without comparison to the original ones there is no way to determine whether any differences

are due to changes in those species' ranges, changes in the analysis of them as species, or whether evolution had perhaps changed them into different species. In short, these ecological remnant models are robust to changes in theoretical perspective on the nature of species.

In order to be robust, several conditions had to be met by the methods for constructing the models. Collecting, note-taking and preserving had to be standardized in order for these "snapshot" ecological models to be collected over time and compared; the materials would also have to be properly preserved for comparison to succeed. This is made all the more difficult in virtue of the goal of real time evolutionary analysis: Grinnell knew he would not live to see the significant results of his own efforts because evolution in nature happens on a longer time-scale than the careers and lives of scientists. Nevertheless, Grinnell was committed to the study of evolution "on the ground, as it happened" rather than by constructing short-term artificial experiments in an indoor laboratory (Grinnell 1910).

Evidence of Grinnell's zeal in standardization can be found in the extent to which he indoctrinated students into his methods. His course handouts beginning in 1913 on how to collect and take field notes cover everything down to the kind and size of paper to use, precisely where and how to enter information on each page, and the brand of ink that *must* be used (Higgins *et al.*). Although seemingly picayune, Grinnell's concern is quite significant: field notes must be curated with the same high standards as specimens if the ecological relations between organisms and environment are to be preserved. Grinnell was so successful in this regard that his student, the mammalogist E. Raymond Hall, published an elaborated version of Grinnell's handout as a manual showing not only Grinnell's method to the last detail, but also that Hall managed to preserve its every detail for 50 years (Hall 1962) (see Figures 1 and 2). Guidebooks describing Grinnell's method are still being turned out (Herman 1986).

Grinnell solved these methodological problems by what I have called vicarious theoretical modeling. To repeat, the theoretical models were themselves material models constructed from remnants of the particular assemblages of animals, plants and environmental factors that intersected in fleeting points in space and time. Grinnell worked doggedly to amass as much data as he personally could, publishing monographic articles running hundreds of pages each. But he worked at least as hard to build an organization, the MVZ, a network of professional and amateur collectors, and a set of institutional practices of collecting, note-taking, labeling, cataloging, preserving and storing. I think he did this as a vicarious means of modeling. Rather than construct all the models himself, which he could not do, he institutionalized his practices in such a way that others could complete what he had begun. If the institution was well-designed, it could persist on the same time-scale as the evolutionary change Grinnell hoped to measure. The vicariousness of Grinnell's specification of theoretical models is thus manifest in the extent to which his methods of museum work were institutionalized. The structure of the models can be studied vicariously as well, by scrutiny of the methodological and institutional writings that specify how models are to be made and of the implementation of those specifications in the organization of research work.

### 3. Wright's Path Diagrams

Sewall Wright developed path analysis as a method for quantitatively assessing the relative degree of influence of variables represented in a system of presumed causal interactions (Wright 1918, 1920, 1921, 1934; cf. Griesemer 1991, Irzik and Meyer 1987, Provine 1986 for review). The method consists of two components: the







formulation of a causal hypothesis by means of a path diagram and the quantitative analysis of relative degrees of influence by the method of path coefficients.

Wright developed the method as an improvement on Pearson's method of partial correlations, which indicated only the aggregate effect of each variable on the total correlation. Wright's method resolved the influence of each variable within a system into components for each specified causal pathway. A path diagram represents variables as letters and indicates causal influence of one variable on another by means of a straight, directed arrow pointing from one to the other. Unanalyzed correlations between variables thought to have influence on a given "effect" variable are represented by curved, double-headed arrows between pairs of causal variables (see Figure 3). Variables are expressed in standardized form, i.e. as deviations from the mean, divided by the standard deviation. Variables are thus treated in abstraction from their units of measurement. On Wright's interpretation, standardization plus the use of diagrams makes each analysis local to the system in which the data are collected and the causal hypothesis depicted.

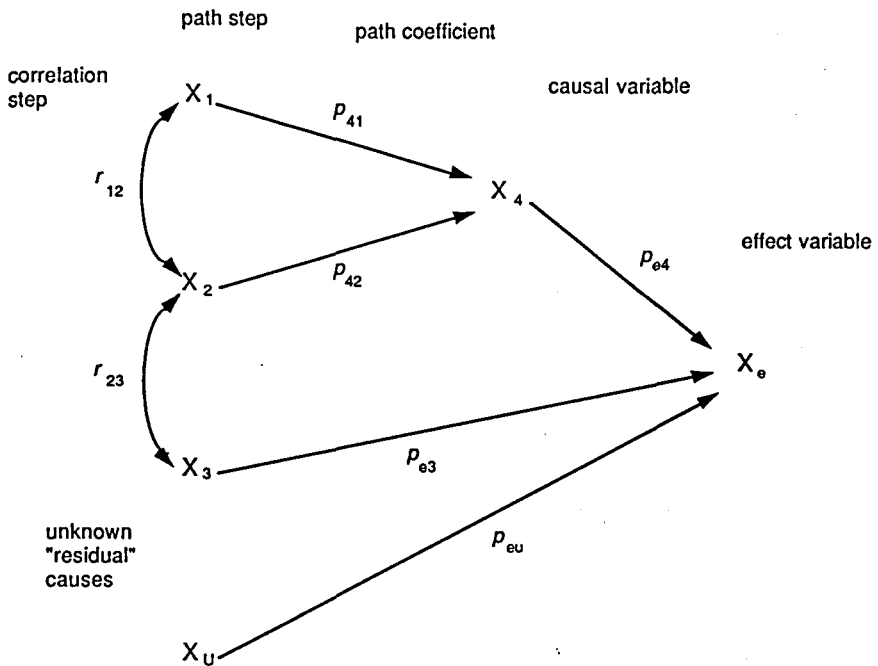


Figure 3. The elements of a path diagram. Note that correlation coefficients ( $r$ 's) are path coefficients ( $p$ 's) for correlation steps. The circuit from  $X_e$  to  $X_4$  to  $X_2$  to  $X_3$  to  $X_e$  is a valid path, while the circuit from  $X_e$  and back that includes both correlation steps is not (by rule 2, see text).

The method of path coefficients involves the construction and analysis of path equations, linear equations in the causal variables weighted by the path coefficients, describing relationships between the standardized variables in the path diagram. Path coefficients are regression coefficients on standardized variables, but path analysis is



not merely regression analysis with diagrams thrown in for illustration. Indeed, Wright (1960) was adamant in distinguishing his method from so-called "causal" regression analysis, as advocated by Tukey (1954). The adamancy takes on significance in light of Wright's view that path equations could be "read off" the diagrams if certain rules were followed. Treating regression and path methods as alternatives, as Tukey did, blurred the distinction between the conceptual role of the path diagram as the causal hypothesis which *generates* path equations with the merely *post hoc* role of an illustration of equations.

Wright distinguished two uses of path analysis: "direct" and "inverse" (Wright 1921). The inverse use deduces path coefficients from measured correlations by solving a system of simultaneous linear equations read from an *a priori* path diagram. The direct use deduces correlations among variables from specified path coefficients (usually given by a previously accepted causal theory) and an *a priori* path diagram. Wright developed the inverse use first, while a graduate student, as a refined analysis of partial correlations in measurements on the bones of rabbits (see Provine 1986, pp. 133-134). The direct use has its most familiar application in Wright's development of a general theory of inbreeding, in which the correlation among relatives is calculated from path coefficients given by Mendel's laws and path diagrams given by pedigree diagrams of descent relations.

The crux of the difference between Wright's path analysis and standard regression analysis is in what sorts of inference are licensed by regression vs. path methods. In regression analysis, the data used to estimate regression coefficients are thought of as population samples and the goal is extrapolation of coefficients for the variables from the sample to the population as a whole. In path analysis, the estimates of path coefficients are relative not just to a sample, but to a particular causal hypothesis expressed in a path diagram. A change in causal hypothesis, i.e. a change of diagram, means that *no* extrapolation from previous data is directly licensed. In other words, concrete, i.e. unstandardized, regression analysis is suited to extrapolation across systems because regression coefficients are estimates for particular *variables* whose component influences in the various causal paths in which they participate is unknown. Path analysis interprets relative causal influence along component *paths* within a system of unitless, standardized variables. This renders variables with different units comparable within the context of a given causal model. Thus regression models are concrete with respect to variables and abstract with respect to systems, while path models are abstract with respect to variables and concrete with respect to systems (Griesemer 1991, p. 166).

For Wright, causal analysis required *a priori* stipulation of a causal hypothesis in a path diagram. Wright developed a set of rules for reading diagrams which allowed construction of correct linear path equations (see Griesemer 1991, pp. 176-180; Li 1975). A path is a valid traversal of a path diagram. Paths may be simple or compound, depending on whether one or more arrows are involved in the traversal. In traversing, one traces the arrows of a diagram and collects the path coefficients: the path is represented by the product of the path coefficients associated with each arrow of the path. Rules for traversal include the following: (1) once a traversal has been made forward along a path (i.e., in the direction of a single-headed arrow), backward traversal is not allowed, (2) traversals along multiple "path steps" (single-headed arrows linked through variables) may be included in a compound connecting path, but only one "correlation step" (double-headed arrow) may be, (3) a path may not traverse a given variable more than once.

For simple systems where the diagram would be simple enough to carry in the head, this rigor is unnecessary: one could write down a correct set of linear equations expressing the antecedent causal hypothesis directly. For more complex systems, it is unlikely that one could maintain a consistent causal hypothesis for the sake of experimentation and quantitative analysis this way. Moreover, at least for many of the sorts of applications Wright envisioned in biology, it is unlikely that a solution to the maximal set of equations would be desired. Indeed, writing just the right subset directly and correctly from a mental hypothesis seems impossible for the complex, irregular systems with which Wright routinely dealt.

There are thus two important reasons for viewing path diagrams as generative. In complex cases, correct statement of a system of statistical relationships that reflect causation can be generated by following diagrammatic construction rules. Moreover, the causal structure deemed implicit in the maximal set of consistent equations for a system is not only isomorphic to the causal structure explicit in the corresponding diagram, but this structure (and all substructures) are easily examined in terms of the latter. Indeed, some numerical questions about statistical relations can even be answered without recourse to equations in the usual sense at all. Calculation can be done simply by collecting term values as one traverses a path diagram visually without writing down equations: the formal apparatus of first formulating an equation symbolically and then setting about solving it is unnecessary. As Wright demonstrated in his development of a general theory of inbreeding, this diagrammatic approach can be generative not only for solutions to specific causal problems, but also for producing concepts applicable to whole classes of path diagrams (in this case systems of mating satisfying Mendel's laws).

#### 4. Weismannism and the Generalization of Evolutionary Theory

My final example concerns the role of Weismannism in the interpretation of Darwinian evolutionary theory as a general theory. Darwinian theory is couched in terms of organisms, but modern evolutionists take the theory to apply to any entities with certain properties (e.g., heritable variance in fitness). While rich in its characterization of certain component processes such as selection, evolutionary theory provides no resources to identify and individuate the entities it is about: nothing in the theory tells us how to determine what count as organisms. Some of this ontological work is done by background theories which are therefore critical for understanding the structure of evolutionary theory.

The modern units of selection literature depends on one of two background theory assumptions in generalizing Darwinian theory: it either assumes a biological hierarchy of levels of organization or it assumes a causal relation between gene-like and organism-like entities expressed in the doctrine of Weismannism (Griesemer submitted). Weismannism is the view that the germinal material forms a continuous lineage while bodies, or somata, do not. The main role of Weismannism in evolutionary theory is to discount the possibility of the inheritance of acquired characteristics (Wilson 1896; cf. Hull 1988 ch. 11). But this is merely one implication of Weismann's theory and some of the others are carried along in its use as a device for generalization (Weismann 1892).

Weismann, it turns out, is no Weismannian. The way in which his theory departs from the standard account and from the modern molecular version of his view is significant for interpreting the character and success of the application of Weismannism to the generalization of evolutionary theory. The moral of the brief story to come is that Weismann's own theory has quite different implications for evolutionary theory

than Weismannism. The latter view has become entrenched in the thinking of biologists and philosophers alike in part because it is presented in a simple and powerful but flawed diagram.

Weismannism expresses a causal asymmetry between germinal and somatic elements and this asymmetry is the basis for various distinctions between the evolutionary roles of “replicators” and “interactors” as generalizations of the concepts of “gene” and “organism” (Dawkins 1976, 1982; Hull 1980, 1981). The evolutionary function of replicators is to directly pass on their structure largely intact in a process of replication. The evolutionary function of interactors is to interact directly with their external environments in such a way that replication is differential (Hull 1980; cf. Griesemer submitted).

The doctrine of Weismannism is most prominently expressed by means of a widely-reprinted and copied diagram due to E. B. Wilson (1896) (see Figure 4; cf. discussion in Griesemer and Wimsatt 1989). The image is further simplified in its modern molecular rendition, made explicit by Maynard Smith (1965) though already implicit in the central dogma of molecular biology (see Figure 5). Wilson’s diagram is ambiguous, however: it could reflect either or both of at least two distinct views: (1) the continuity of the germ-cells and discontinuity of the somatic cells, or (2) the continuity of the germ-plasm and the discontinuity of the somato-plasm. It is clear from the discussion in Wilson (1925) that he interpreted Weismann to mean the former, lumping Weismann’s view with contemporaries who held to the former. But Weismann explicitly rejected this interpretation (Weismann 1892; cf. Griesemer and Wimsatt 1989). Maynard Smith’s diagram, on the other hand, is unambiguously wrong of the view Weismann himself held even if we factor out the modern interpretation of the molecular constituents of germ-plasm (Griesemer submitted).

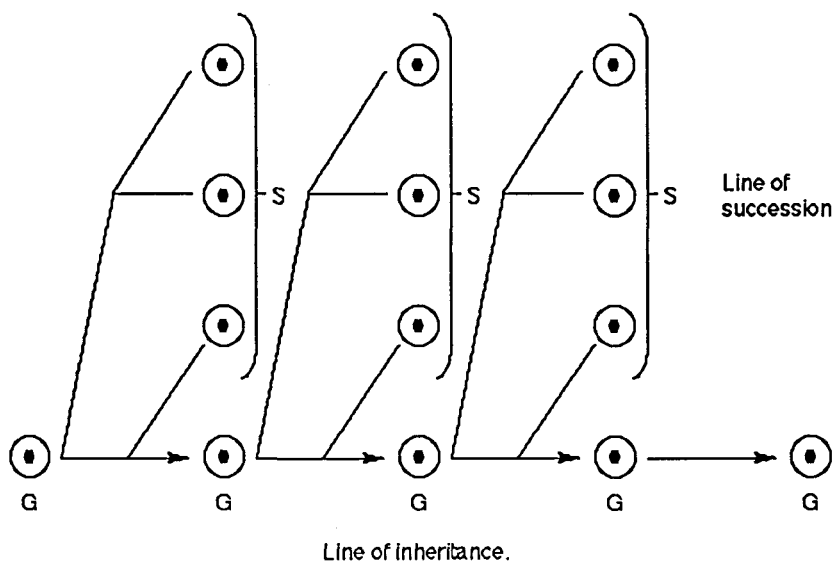


Figure 4. E.B. Wilson's representation of Weismannism, after Wilson (1896, p. 13, fig. 5).

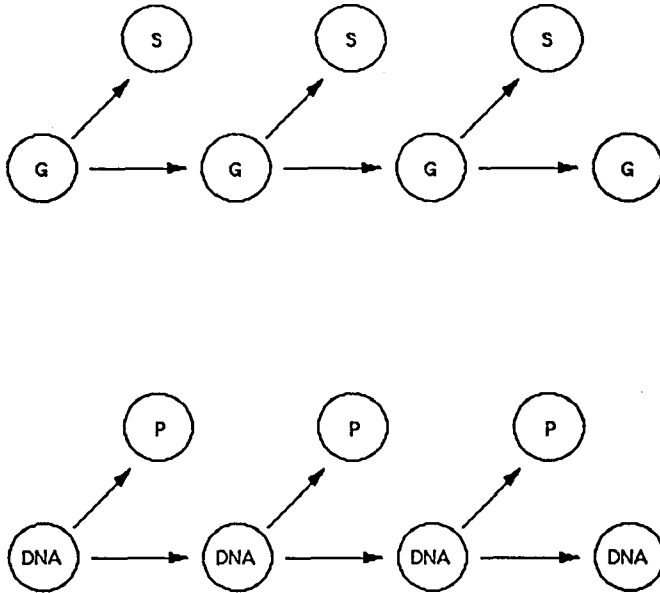


Figure 5. A simplification of Wilson's representation of Weismannism compared to a modern molecular representation of the central dogma of molecular biology, after Maynard Smith (1965, p. 67, fig. 8).

Moreover, it is clear from Weismann's own very different diagrammatic representation of his theory that he held the germ-plasm rather than the germ-cell view (see Figure 6). For Weismann, germ-cells were products of somatic differentiation, just like every other cell in the body. This is shown in his diagram in virtue of the fact that germ-cells first appear in the developing worm depicted in cell generation 9 (the cells are labeled "urKz", urKeimzellen). It follows that germ-cells do not form a continuous lineage, they are interrupted in development by a series of somatic cells, just as organismal bodies are interrupted in descent by their passage through gametes that must combine (in sexual species) to form zygotes. What is continuous is the molecular germinal protoplasm in the nucleus of the cells fated in development to become germ-cells. The implication of this fact is that the phenomena of heredity must ultimately be explained in terms of development. Thus, for Weismann, the problem of explaining hereditary transmission of germ-plasm is a problem of development, not an autonomous problem to be treated separately from development, as is represented in Wilson's diagram with a separate continuous line for germ-cells and a discontinuous "line of succession" for somata.

Returning to the problem of generalizing evolutionary theory, if the goal is to rely on a background theory to abstract causal roles that must be fulfilled for evolution to occur, then Weismannism is a bad choice for two sorts of reasons. First, it gets the facts about genes and organisms wrong (Griesemer submitted). Second, and more significantly, it gets the abstract structure of the causal relations between genetic material and somatic material wrong. If hereditary transmission is controlled by somatic development, then there are causal arrows from soma to soma (ibid.). This does not imply, however, that the flow of genetic information in its currently evolved state is



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