

Structural Realism in Biology: A (Sympathetic) Critique

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Structural realism holds that ontological commitments induced by successful scientific theories should focus on the structures rather than the objects posited by the theories. Thus structural realism goes beyond the empirical adequacy criterion of traditional (or constructive) empiricism. It also attempts to avoid the problems scientific realism faces in contexts of radical theory change accompanied by discordant shifts in posited theoretical objects. Structural realism emerged in the context of attempts to interpret developments in twentieth-century physics. In a biological context, Stanford (2006) provided pre-emptive criticism. French (2011, 2012) has since attempted to answer those criticisms and extend structural realism to the biological realm. This paper argues that, though Stanford's criticism may be misplaced, and structural realism fares much better than traditional scientific realism in biological contexts, it remains a promissory note. The promise is based on shifting the focus of the debate from the status of biological laws to that of biological organization, an issue that remains a live debate within biology.

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1. *Introduction*

Structural realism is conveniently decomposed into four related claims which form a sustained argument. Let the entities posited by a scientific theory or model¹ consist of two types: objects and structures, for

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¹ Throughout this paper, theories and models will be assumed to be entities of the same logical type, differing only in the generality of their intended domains. There is a body of philosophical literature that distinguishes between the so-called syntactic

instance, diachronic or synchronic relationships of varying complexity that hold between the posited objects. Typically, the dynamical possibilities allowed by the theory or model (what may happen over time) will be incorporated into these structures (in terms of rules governing them). The four components of structural realism are:

1. The history of science, especially in cases of radical theory change, shows that the (theoretical) objects² postulated even by empirically well-confirmed theories often disappear and are replaced by radically different ones—consider examples such as vortices, the caloric, phlogiston, ether, and protoplasm.
2. This aspect of scientific change critically undermines any ontological commitment to objects postulated by theories whether this commitment is only about what can be known (an epistemic claim) or about what there is (an ontic claim).
3. In contrast, some of the structures posited by theories, for instance, the laws governing the putative objects, are often resilient across radical theoretical change. The second law of thermodynamics, for instance, survived the transition from the caloric theory to classical thermodynamics and even to the kinetic theory of matter; so did many of the known chemical laws during the transition from phlogiston to oxygen.
4. Thus, in contrast to the situation with theoretically posited objects, there is ample ground for ontological commitment to the theoretically posited structures of well-confirmed theories even in the face of radical theory change.

Part (4) encapsulates the central claim of structural realism which is presumed to be a consequence of the first three parts.

The epistemic version of structural realism holds that the relevant structures comprise all that can be known; the ontic version, which is the principal locus of contemporary structural realist research, claims that these structures are all that there is (independent of any particular theories about them). Either version avoids the pitfalls of the object-oriented scientific realism that came into vogue in the 1960s and 1970s in the early post-logical empiricist philosophy of science following a general (and, perhaps, misguided) rejection of the instrumentalism associated with most of the logical empiricist canon. Structural realism also goes beyond traditional empiricism in denying incorrigible phenomenal content as the epistemic foundation for scientific knowledge and, especially, by not accepting a criterion empirical adequacy as the

and semantic interpretations of theories, with “models” supposed to be related to the latter; however, neither the goals of that project, nor the many problems with such accounts, are relevant to the issues treated in this paper. Most importantly, the usage here follows standard scientific usage in biology (and elsewhere)—see Frigg and Hartmann (2006).

² The term “object” must be construed broadly to include any non-relational entity (particle, field, cell, information, community, carrying capacity, *etc.*).

sole desideratum for the adjudication of theoretical commitment, the latter position being closely associated with constructive empiricism (van Fraassen 1980).

Historically, structural realism was developed with the goal of providing a viable realist interpretation of modern (twentieth-century) physics taking into account the profound conceptual changes induced by quantum mechanics as well as the special and general theories of relativity. Stanford (2006) pre-emptively criticized its applicability to biology as part of a general critique of realism about science. French (2011, 2012) attempted to answer those criticisms and extend structural realism to the biological domain. This attempt is usefully analyzed into two separate theses: (i) a critique of object-oriented realism about biology; and (ii) a tentative defense of realism about structures interpreted as biological laws³ which, though admittedly lacking universality, apparently remain resilient under many theoretical changes.

The purpose of the present paper is to offer a critical assessment of structural realism in biology. Because structural and any other forms of realism are easy to criticize on purely philosophical grounds, especially when divorced from the practice of science, and when no alternative need be provided, Section 2 will sketch a set of positive theses that are supposed to criticize structural realism and fare somewhat better at interpreting contemporary biology. As a consequence of that discussion, Section 3 will largely endorse French's skepticism about object-oriented realism in biology but emphasize several subtleties that dilute the impact of his critique. However, and more importantly, it will also extend this skepticism to the biological laws favored by French in his defense of structural realism in biology. Section 4 will turn to the role of organization—and that sense of structure—in the history of biology, and in contemporary biology, and argue that this is where structural realism is most plausible in biology. Section 5 will question whether, even in its most plausible domain, prospects for structural realism in biology are better than dim. It will be inconclusive. Ostensibly to compensate for that, Section 6 will draw some conclusions.

2. *Positive Agenda*

It will be instructive to begin with the putatively central insight of structural realism: that certain structures (for instance, relationships between putative objects) persists over radical theory change, radical in the sense that the objects postulated by the earlier theory do not survive the same transformation. This point will be illustrated in this section using an example that instrumentalist critics of structural realism have deployed in favor of their own position, *viz.*, Galton's biometrical

³ It is open to question whether structures should necessarily be interpreted as laws or even as relationships between (adequately individualized) objects. I follow French on this point for *biological contexts*. Nothing in French's discussion—or mine—restricts structures to laws or relations.

Law of Ancestral Heredity.⁴ The discussion here will bring that use of this law into question.

However, before turning to the details of that example, it is worth emphasizing (with French [2011, 201]), the general non-persistence of theoretical objects in biology. Take perhaps the single most important such object of twentieth-century biology: the gene. Two points, both of which deserve much further elaboration than will be possible here, are of relevance: (i) It is far from clear that “gene” continues to play *any* theoretical role, rather than an informal heuristic one, in contemporary postgenomic accounts of heredity.⁵ Arguably, in explicit theoretical discussions of DNA behavior during cell reproduction and differentiation, the concept of a gene has no more a cognitive role in contemporary biology than what the concept of an electron orbiting a nucleus has in contemporary chemistry. If this is correct, even though much of the insights of classical genetics, in the forms of rules of transmission and expression of traits, continue to remain relevant, during the last two decades the gene has lost its pre-eminent ontological status that it had in biology for almost a century (Keller 2002b). (ii) To the extent that certain DNA sequences can still be usefully characterized as traditional genes (most importantly, some of that tiny fraction of DNA in most eukaryotes that uniquely specify amino acid sequences of proteins⁶), these objects share as few properties with Johannsen’s (1905) original “genes” as today’s atoms do with Dalton’s creation. For instance, thanks to ubiquitous alternative splicing, a single gene may often specify more than one phenotype (at least at the protein level). Stein (1989) has aptly pointed out that to assume the “reality” of the atom and not, say, of the ether on the basis of the persistence of one term and not of the other is no more than a surrender to the vagaries of changes in linguistic usage. The same point can be made about the persistence of “gene”; an even stronger case can be made against another pillar of mid-twentieth century molecular biology: biological “information” (Sarkar 1996).

In contrast, turn now to a discarded tradition in the study of heredity that once held considerable promise: Galton, Weldon, and Pearson’s science of biometry.⁷ Galton posited the existence of a “stirp” in the

⁴ This example is important in this context because it forms part of Stanford’s (2006) critique of structural realism which will be discussed later in the text. For a more detailed philosophical analysis, see Sarkar (1998, Chapter 5).

⁵ See Perini (2011) for a good discussion and an entry into the extensive literature.

⁶ The qualification “some of” is necessary to exclude overlapping genes, *etc.*—see Sarkar (1996) on this point; the qualification “uniquely” similarly avoids problems associated with alternative splicing. The qualification “traditional” is necessary because it is not at all unusual to refer to any functional DNA segment as a gene (*e.g.*, Lynch [2007], Koonin [2011], *etc.*), no matter whether it is transcribed and translated, transcribed but not translated, or even plays a regulatory role in some other way—this is the heuristic or informal notion of a gene noted earlier.

⁷ The best summary is Pearson (1900); Provine (1972) and Sarkar (1998) provide historical and philosophical discussion.

germinal cells of organisms which mediated the inheritance of traits from parent to offspring. On the basis of this model of inheritance, he postulated several nomological claims, the most famous of which was the quantitative Law of Ancestral Heredity which, after subsequent clarification and reformulation by Pearson, states (roughly) that the ancestral contribution to any hereditary trait of an individual organism decreases in a geometric series with distance up the family tree.⁸ The biometricians were (correctly) adamant that a wealth of quantitative empirical data on continuously varying traits from the 1880s and 1890s supported the Law of Ancestral Heredity.

It is uncontroversial that the theoretical claims of biometry—in particular, Galton’s stirp model of inheritance (to the extent it should even be taken to be part of the science of biometry)—were superseded and replaced by Mendel’s model of inheritance shortly after Mendel’s work was recovered around 1900, and after an acrimonious dispute between adherents of the two sides with the Mendelians represented primarily by Bateson but with support from others including Punnett.⁹ Yet, as Olby (1966, 1987) and others have periodically pointed out, the mathematical relationship incorporated in the Law of Ancestral Heredity, interpreted as a correlation between traits of an organism and its ancestors (rather than as a “contribution” from ancestors), continues to hold in a Mendelian¹⁰ context.

This would seem to be grist for the structural realist’s mill. Stanford (2006: 182), however, is dismissive; according to him, what Olby’s observation (and others that are similar) show is that:

“the formal relationship described by the Ancestral Law [*sic*] can certainly be unearthed by sufficiently persistent digging into the corners of the theoretical description of the world given to us by contemporary genetics.

But it is equally true that contemporary genetics does not recognize the fractional relationships expressed in Galton’s Ancestral Law as describing any fundamental or even particularly significant aspect of the mathematical structure of inheritance.”

Stanford continues with a dismissal of Worrall’s (1989) version of structural realism.

Though the neutrality between realism and instrumentalism that I generally endorse shares some of Stanford’s skepticism about realism, his dismissal of the Law of Ancestral Heredity is unwarranted. Any serious history of the Law of Ancestral Heredity must pay more attention to the pertinent detail. Pearson’s reformulation of the Law of

⁸ Galton’s (1965) first rudimentary statement occurs in the work taken to be the origin of eugenics, “Hereditary Talent and Character”; Pearson’s final statement appears in the second edition of *The Grammar of Science* (Pearson 1900).

⁹ This has been extensively documented by Provine (1971).

¹⁰ The term “Mendelian” instead of “Mendel’s” is being used to distinguish between what became part of the new (Mendelian) genetics between 1900 and 1920 and Mendel’s own statements which required considerable modification during the formulation and establishment of what came to be called Mendelian genetics.

Ancestral Heredity involved two related crucial philosophical moves: (i) He dropped the stirp model altogether and eschewed causal talk (of “contribution”) in favor of correlation between traits. So, whether or not Galton’s stirp model of inheritance (which constitutes an object-oriented ontology) is correct becomes irrelevant to the status of the Law. (ii) In general, Pearson insisted that, in the historical context in which biometry was attempting to construct a quantitative theory of evolution by natural selection, the laws of heredity should remain what will be called *phenomenological*. This move to phenomenological characterization was a consequence of Pearson’s quite sophisticated positivism—but that is a story for some other occasion.

By “phenomenological” here I mean laws that employ the same (or very similar) conceptual resources as those deployed to report the results of experiments. This is a matter of degree. Some claims are more phenomenological than others; in that sense they are less theoretical than those others. Note that there is no claim here of any hard observational-theoretical distinction. How experimental reports are formulated depends on what theories are taken to be sufficiently well-established so as not to be challenged by the experiments being performed. What is at stake here is that, in the given context of research, phenomenological resources can be used to formulate claims that can be used to adjudicate between the theories that are in play. Returning to the example at hand, the Law of Ancestral Heredity, interpreted phenomenologically, could potentially be used to distinguish between Galton’s and Mendel’s models of inheritance. Historically, it turned out to be the case that it is consistent with both in the sense that both models *semi-formally* predict it, where mathematical predictions are deemed to be “semi-formal” if they require idealizations or incorrigible approximations.¹¹

What is more important in this context is that the Law of Ancestral Heredity was taken to be sufficiently empirically well-supported to impose constraints (adequacy conditions) on permissible theorizing about heredity in the 1900–1920 period: any adequate theory of heredity had to incorporate that Law. This is seen, in particular, by Pearson’s (1904a, b) own attempts to derive the law from Mendel’s rules as well as Doncaster’s (1910) review of recent work in heredity which discussed both Mendel’s rules and the Law.¹² When Fisher (1918) began his ambitious project of using Mendel’s rules to account for inheritance patterns of continuously varying traits—what led to the subsequent discipline of quantitative genetics—it was still perceived to be critical to establish consistency between the Law of Ancestral Heredity and Mendelian

¹¹ Here “incorrigible” means that there is no known procedure to weaken the relevant approximation—for a discussion, see Sarkar (1998: 49).

¹² Even by 1920 Doncaster had not changed his mind—see Lock and Doncaster (1920).

rules¹³, hardly something to be dismissed as “persistent digging into the corners of the theoretical description of the world given to us by contemporary genetics.” What Fisher showed was remarkable: the Law of Ancestral Heredity could be semi-derived from Mendelian rules.¹⁴ An entire section of “The Correlation between Relatives on the Supposition of Mendelian Inheritance” (§ 17) was devoted to deriving that Law from Mendelian assumptions. It amounted to a reduction of the Law of Ancestral Heredity to Mendelian genetics. In fact, what Fisher achieved was the reduction of all the more salient nomological claims of biometry to a Mendelian basis. This included, for example, the rule that quantitative traits follow the normal distribution in large populations.¹⁵ After Fisher’s derivation the empirical status of the Law of Ancestral Heredity was no longer in question: evidence for Mendelian genetics was *ipso facto* evidence for that Law (at least informally).¹⁶ What changed was that all the biometrical generalizations proved to be of decreasing utility in practical contexts of quantitative genetics, the most important ones being those of agriculture and animal breeding.

Structural realists will interpret this situation as indicating that though there should be no ontological commitment to theoretical objects (Galton’s stirp of Mendelian genes), there are grounds for such commitment to the relevant structures, that is, associated laws such as the Law of Ancestral Heredity. This position can be bolstered using a wealth of examples from the physical sciences including, as noted earlier, the persistence of the second law of thermodynamics in the transition from the caloric theory to classical thermodynamics (incorporating the first law, or conservation of energy). Contrary to Stanford (2006), such an interpretation of the significance of the persistence of the Law of Ancestral Heredity is hardly far-fetched.

What skeptics of structural realism must do is to provide a more *scientifically* compelling interpretation of these developments (in the sense of a more plausible interpretation of history and practice in the relevant scientific episode). What follows is a sketch such a position, one which is supposed to provide a contrast to structural realism but does not endorse any form of anti-realism (including constructive empiricism). Rather, partly following and extending the discussions of Nagel (1961) and Stein (1989), it sees no essential difference between

¹³ Fisher was neither the first nor the only geneticist to acknowledge this requirement: Yule (1902) and Weinberg (1909a, b; 1910) were among those who preceded him—Stern (1965) provides an illuminating discussion of these developments.

¹⁴ For critical discussion, see the commentary by Moran and Smith (1966) and the discussion in Sarkar (1998, 106–107).

¹⁵ This aspect of the creation of quantitative genetics is discussed in more detail by Sarkar (1998, Chapter 5). See, also, Frogatt and Nevin (1971). But much more philosophical analysis would be welcome—and would not go unnoticed.

¹⁶ In general, evidence for a reducing theory is indirect evidence for the one that is reduced (Sarkar 1998).

a sophisticated instrumentalism and a modest version of structural realism which is closer to the epistemic rather than ontic version. Ultimately, the force of the critique of structural realism being developed here should be taken to rest partly on the plausibility of this alternative view.

It will serve to present this alternative position as being constituted by four distinct substantive points followed by one polemical one which is of less importance:

1. With structural realism, it agrees that the history of science makes it impossible to defend any ontological commitment to theoretical objects (object-oriented realism).
2. Again with structural realism, it agrees that the certain structures are more resilient across theoretical change than objects. In the biological context these structures include (but are not limited to) laws though not all laws have the required degree of resilience.
3. Unlike structural realism, the resilience of these laws is explained by their phenomenological status in the context in which they are introduced or used to adjudicate between rival theories. This is a central tenet of the position being advocated here and some elaboration seems in order. In a given historical context, phenomenological laws are supposed to be theoretically neutral in the sense that the theories being adjudicated do not differ in their predictions (or otherwise) with respect these laws. By and large—and this a claim subject to historical test—in further development of a field, laws that were deemed phenomenological in one context will remain so in future contexts because it seems implausible that they will become “theory laden” with newer, typically more abstract, theoretical assumptions.¹⁷ Thus, phenomenological laws form part of what each successive theory must explain. Consequently, they are often resilient over theory change.
4. Nevertheless, phenomenological laws need not have indefinite tenure. For instance, radical theoretical—or even experimental—change may show that the degree or type of approximation involved in accepting a phenomenological laws may make it contextually no longer admissible to deem such a law as (approximately) correct. In Section 3 it will be argued that this is, indeed, the situation of the Law of Ancestral Heredity in the light of postgenomic developments. There is no evidence in biology that there is convergence to any set of phenomenological laws that appear so safe from future rejection (or, at least, radical revision) to warrant deep ontological commitment. Indeed, if structural realism is committed to such laws as the only relevant structures, it will not fare better than object-oriented realism.

¹⁷ Note the qualification, “by and large”—this is not being presented as an exceptionless claim.

5. The final point is polemical and historical—the cogency of the arguments presented here does not depend on its validity but it help show what, at least partly, motivates this position. Points 3 and 4 have much in common with logical empiricism, in particular, the views of Neurath, Reichenbach, and Nagel. What are being called phenomenological laws here are generalizations of what the logical empiricists called protocol sentences expressed in a physical language (the generalization being that these phenomenological laws are universally quantified over the relevant domain). Like protocol sentences, these laws are corrigible though, unlike protocol sentences, they are not the sole epistemic basis for the relevant theoretical models.¹⁸ The attitude towards ontological commitment expressed here is also similar to that of those logical empiricists who endorsed some form of “realism” but saw it as being consistent with their empiricism in contrast to the types of realism associated with object-oriented or structural realism.

The scope of this alternative position is at present intended to be limited to biological contexts in which there are no known “deep” structures (such as symmetry groups in some physical contexts) which cannot be easily interpreted as phenomenological laws.

3. *Biological Laws and Structural Realism*

As noted earlier, a case against object-oriented realism in biology could have made profitable use of examples such as the gene or information. Equally apt ecological examples would include carrying capacity, climax community, and intrinsic growth rate. In developmental biology terms that have undergone radical shifts of empirical significance include “genotype” and “norm of reaction” (Sarkar 1999). However, the only published defenses of structural realism in biology (French 2011, 2012) rely on Dupré and O’Malley’s (2007, 2009) critique of biological individuality as delimiting a unique set of (biological) objects. There are two pitfalls with this line of argument:

- (1) Dupré and O’Malley’s concerns are synchronic, to deny *at this time* the possibility of a unique ontology of well-defined objects constituting the biological realm. Instead, they opt for pluralism and what is called a “promiscuous realism” (Dupré 1996) about objects. Leaving aside a discussion of the plausibility of promiscuity for some other occasion, in this context what is at stake is the diachronic identity of objects across theory change because that is what structural realism denies. The problems raised by Dupré and O’Malley are tangential to this issue.

¹⁸ Rather, they are the *explanans* in Nagel-type models of reduction (see Nagel [1961]).

- (2) The second problem is both philosophically and biologically more important. Long ago, Nagel (1951, 1952) pointed out that any mereological decomposition of an object requires theoretical assumptions. Objects do not simply exist in a categorical spatial hierarchy; rather, to say that a given object consists of a specified set of parts is to make a theoretical claim, one choice among others about how to decompose a whole into its parts. The cogency of a decomposition depends on the empirical success of this theory along with the relevant theoretical claims about the behaviors of the whole and the parts (including their interactions). While Nagel made this perceptive observation in an explicitly biological context, it is relevant to all scientific contexts in which hierarchical organization is presumed. The biological context introduces an added complexity: the wholes, as well as the parts, are themselves (a) historically evolved objects¹⁹ that (b) must be individuated using theoretical criteria—that is, beyond Nagel, even what the whole is requires theoretical specification. Physical individuals need not be organismic individuals: in most physical mammal bodies the vast majority of cells are not those of the mammalian individual *qua* mammal. (Consider, for instance, the human skin or intestine—there are 10 times as many non-human cells in the latter as there are human cells in a typical body [roughly 10^{14} of the latter].) Genotypic individuals need not be physical individuals, *e.g.*, in the cases of dandelions or aphids. In fact, what Dupré and O'Malley's (2007, 2009) analyses show is the ubiquity of the individuation problem in the metagenomic context (which is not unexpected).

To make a case against object-oriented realism on the basis of problems of biological individuality will require (i) the specification of a theoretical individuality criterion (genotypic, immunological, organismic, *etc.*) and (ii) a demonstration of the diachronic ephemerality of these individuals across theory change. French does not do this, and it remains an open question whether biological individuals, however defined (so long as these definitions are exact and explicit), are as ephemeral as, say, genes or information.

The last paragraph may well have been a digression from the argument of this paper since it agrees with structural realists that an ontology of biological objects is far too unstable to warrant “realism.” What is more problematic for French's argument is the question of the resilience of biological laws. It will be instructive to return to the Law of Ancestral Heredity. It was pointed out in Section 2 that the fundamental mathematical (read “structural”) claim of that law, that is, the geometric regression of correlation with ancestral relatives, survived the transition from biometry to (Mendelian) quantitative genetics.

¹⁹ See, in this context, Buss (1987) and the commentary by Falk and Sarkar (1992).

The potential trouble is that the postgenomic era is witnessing a much more radical shift in the understanding of heredity than the shift from biometry to Mendelism (though the ongoing shift is as yet poorly understood even within biology, let alone in the philosophy of science). It was noted in Section 2 that few DNA sequences exhibit Mendelian patterns of inheritance. Add to this (i) that horizontal DNA transfer across lineages has been ubiquitous in early evolution (which, either in the number of years or in the number of generations, has been the longest period of evolution), (ii) large DNA sequences often duplicate during reproduction (and this process is now widely recognized as being critical for the generation of evolutionary novelty), and (iii) genomes tend to expand through a variety of molecular mechanisms due purely to the physics of DNA interactions (Lynch 2007). It is questionable that the Mendelian rules will survive this transition except as approximations applicable to a tiny fraction of inherited traits (though these are the ones that dominated research in twentieth-century biology because the Mendelian rules they followed made them easily tractable). It appears unlikely—though this is as yet unproven—that the Law of Ancestral Heredity will survive this ongoing transition any better; worse, given that it is an approximation even in a Mendelian context, it will become irrelevant. The philosophically salient point is that even phenomenological laws do not have indefinite tenure though they generally have longer ones than theoretical objects.

A potentially more interesting “law” is the Price equation on which French (2012) aptly focuses. This equation, which has recently been the focus of sustained interest within evolutionary biology (Frank 2007), began its remarkable career as an intended reformulation of what Fisher (1930) called the fundamental theorem of natural selection (Price 1972). However, it turned out to be more general in two important ways: (i) it can recursively incorporate the operation of selection at multiple levels of a hierarchy, and (ii) it does not depend on the details of the Mendelian model of inheritance. This generality makes the Price equation more akin to a constitutive framework in which a variety of laws can be formulated (or, equivalently, models can be constructed) than to an individual law—this point will be relevant in Section 6.

But there are ample grounds at least for caution, perhaps downright skepticism. While Fisher regarded his theorem as fundamental, and a minority cadre of very vocal theoretical population geneticists have followed him in extolling its virtues, it should not be forgotten that the other two major founders of theoretical population genetics, Haldane (1932) and Wright (1930), were skeptical of its significance (Edwards 1994). If taken as an exact claim, that is, its mathematical form is supposed to capture the operation of selection *in toto*, the assumptions of the theorem hold for vanishingly few cases. The same problem carries over to the Price equation: more technically, both Fisher’s theorem and the Price equation make strong and debilitating assumptions of the

additivity of the effects of alleles (or their equivalents at other levels of organization).²⁰ Now, if Fisher's theorem and the Price equations are taken to be approximate, then it is less than clear what ontological significance should be attached to the persistence of such a structure. (However, both the theorem and the equation now become applicable to many more situations.) A way out would be to regard either of them as an idealization but then it would be one requiring a host of counterfactual assumptions: it is up to structural realists to show how such extreme idealizations can ground deep ontological commitments. This may not be an impossible task. Meanwhile, at present, there is ample ground to doubt the significance of the Price equation—moreover, and perhaps most importantly, what will happen to it in post-genomic accounts of heredity also remains far from clear. It takes a lot of faith to assume it will be resilient in the way that structural realism requires. Worse, no other putative biological law provides better prospects for structural realism.

4. *Biological Organization and Structural Realism*

The failure of biological laws to underpin structural realism does not sound the death knell of that doctrine in the biological context. Rather, structural realists would do well to focus their attention on biological organization. This means a shift of focus from what may be called nomological particulars (individual laws) to constitutive frameworks in which these nomological claims can be formulated.²¹

Historically, two distinct themes have been important:

- (1) Since the late eighteenth century, and even after the demise of traditional vitalism in the nineteenth century, biology has persistently accommodated research programs based on the assumption that biological organisms have some feature(s) that distinguish them from what may be called purely physical (or chemical) structures. In general, there was no claim that biological organisms exhibited mechanisms at variance with the known physical (and chemical) ones; rather, invoking only these mechanisms was deemed insufficient for the satisfactory explanation of biological phenomena. The various research programs that incorporate such assumptions may be distinguished into two groups²²:

²⁰ See, however, Frank (1997) who defends the additivity assumption but nevertheless accepts that it imposes some restrictions.

²¹ That is, within a constitutive framework, a variety of laws can be formulated. Typically, in biological contexts these laws are called models.

²² The characterizations given here intentionally avoid the issue of reductionism which will be fully broached in Section 5.

- i. Teleological holism, discussed in Section 4.1, which emphasizes function and teleology in a way that was supposed to subordinate the relevant explanatory behaviors of parts to goals that were only specifiable by reference to the whole.
- ii. Structural emergentism, discussed in Section 4.2, which emphasizes what is typically referred to as the emergence of systemic properties which are supposed to be at variance with the properties of the constituent parts of these systems.

(2) Since the nineteenth century there also has been a long—and, at least arguably, so far futile—search for laws of form: principles of structural organization which are supposed to explain what Raff (1996) called the “shape of life.” These laws of form are supposed to explain why, for instance, all animal embryos at an early stage of development have either two-fold or five-fold symmetry (and no other). The salient research programs will be discussed, though only very briefly, in Section 4.3.

In the present context, what is relevant is that these research programs emphasize structure over objects. In the case of developmental form, the structure is clearly spatial; in the cases of teleological holism and structural holism, the structure may be embedded in an abstract space but may also be spatial in nature, as is usually the case for the structural emergentists. The details that follow are intended to show why these programs *may* support structural realism.

4.1. *Teleological Holism*

An epistemological characterization of the assumptions of research programs subsumed under this category is relatively straightforward. Organisms (or other wholes) are supposed to be categorically described as having goals. Here “categorically described” means a type of description that is necessary to understand these organisms (wholes) *qua* organisms (wholes). In some form or other, such a view of living organisms can be traced back to Aristotle; it is a plausible (and was a popular) interpretation of the second part of Kant’s *Critique of Judgment*. With Kant, nineteenth-century teleological holists such as von Baer generally held that the mechanisms operating within living organisms were no different than those also operating in non-living matter.²³ However, to explain living phenomena satisfactorily required reference to the goals of the whole: why a part does what it does depends on its structural relationships with other parts with which it forms a whole; these relationships establish its functional contributions to the goals of the whole. Consequently, any determination of the set of

²³ A complex history is being selectively summarized—and perhaps caricatured—here for philosophical purposes, possibly to the extent of parody. See Lenoir (1989) for more detail.

mechanisms that are explanatorily relevant to the living phenomena that are to be explained must take into account how the parts are structured so as to comprise the whole. As Lenoir (1989: ix) puts it: this was “a period in the history of the life sciences when the imputation of purposiveness was not regarded an embarrassment but rather an accepted fact, and when the principal goal was to reap the benefits of mechanistic explanation by finding the means of incorporating them within the guidelines of a teleological framework.” A more radical version of these claims would go further to argue that what the parts are is relatively irrelevant compared to the structure: this is the form that teleological holism took under the guise of cybernetic models in the mid-twentieth century (see below). An ontological characterization of these doctrines adds an ontological gloss on the claims of this paragraph (but does not change any other feature).

The mid- and late nineteenth century saw the relentless progress of mechanistic explanations in the life sciences, that is, explanations of the properties of wholes from those of their constituent parts and their interactions (Sarkar 1998). Nevertheless, a form of teleological holism became fashionable in physiology through sustained advocacy by Bernard (1865) and his insistence that the physiological behavior of parts of an organism could only be understood in terms of the context in which these behaviors occurred, the context being specified by the other parts of the functional whole. Other physiologists including Christian Bohr and J. S. Haldane in the early twentieth century explicitly embraced similar doctrines.²⁴ The critical assumptions were (i) that physiology was intrinsically about function and (ii) that function could only be understood by subordinating the behaviors of parts to that of the whole. Of particular interest were co-operative phenomena, in which the increase in the number of units results in a non-linear increase of effect, for instance, the S-shaped association curve between hemoglobin and oxygen that Bohr established (the “Bohr effect”). These cases often displayed feedback regulation—a drop in the response after saturation with oxygen, a feature seen in the S-shape of the hemoglobin-oxygen association curve. Structurally what mattered is how the system was constructed together and how the parts with their functions interacted with each other. In this sense these views were very similar to those of teleological holists of the nineteenth century (and, by and large the physiologists were explicit in admitting the influence of Kant’s third *Critique*).²⁵ The term “holism” was coined later by Smuts (1926), though mainly in an evolutionary context, to embrace these views.

Meanwhile, the emergence of biochemistry as an organized discipline under G. W. Hopkins in the 1920s and its empirical successes saw

²⁴ See J. S. Haldane (1906, 1914); on Bohr, see Tigerstedt (2012). Their views also had an influence of the non-mechanistic theses promoted by their more famous offspring: Niels Bohr and J. B. S. Haldane (Holton 1970; Sarkar 1992b).

²⁵ See, for example, J. S. Haldane (1914).

mechanistic explanation return to the forefront in contexts in which holistic physiology had once reigned unchallenged (Sarkar 1992a). However, models of feedback regulation, beginning in the mid-1950s, typically based on Wiener's (1948) cybernetics, gave teleological holism a new lease of life.²⁶ The self-regulation of enzyme (more specifically, lactase) production in bacteria (*Escherichia coli* in this case) in the presence of the relevant substrate (in this case, lactose) emerged as a problem of experimental investigation²⁷—the result was the operon model, the significance of which will be further discussed in Section 5. Monod (1971) later dubbed this work as “molecular cybernetics.”²⁸ Suffice it to note that the interest in the regulation in biological systems has had a continuous history since the 1950s resulting in the current emphasis of gene regulatory networks (GRNs); some of these developments will be taken up in more detail in Section 4.2.

In the present context what is most salient is the extent to which such models of self-regulation make specific (that is, detailed) and general (that is, applicable to a wide variety of cases) assumptions about structural organization. Historically, at the very least, these models universally assumed a network structure of interactions between the unit components constituting the whole (that is, the interactions could not be reduced to a single chain), and typically assumed loops (enabling feedback). It can be assumed without loss of generality that the mathematical structure required by these models is that of a directed multigraph²⁹ (which, for ease of formal analysis, is typically reduced to a directed graph). The structural realist thesis is now straightforward to state: the edge sets, that, is their topological or connectivity features (what types of connections there are), will show resilience across theory change even when the identity of the vertex set changes. If so, in such models, the explanatory weight (however that is explicated) is borne by the structure rather than the objects—as structural realism would require. There will be more on networks and multigraphs in Section 4.2 below.

4.2. *Structural Emergentism*

The focus will continue to be on networks modeled as directed multigraphs. However, there is a critical difference between the research programs considered here and those mentioned at the end of the Section 4.1. The models analyzed here do not insist on some special role

²⁶ The importance of cybernetics to mid-twentieth-century science is hard to understand today (because of its apparently total failure) but can hardly be overstated—see Heims (1991).

²⁷ Schaffner (1974) provides a detailed history.

²⁸ Sarkar (1996) provides background.

²⁹ These differ from ordinary graphs insofar as edges and vertices can be of more than one type; thus, for instance, more than one edge (each of a different type) can join two vertices.

played by the goals of function of the whole or on whether explanations using constituent parts must refer to the wholes. There is no explicit teleology in these models. Instead, most (though not all) such models are concerned with whether the topology of the edge sets are more strongly implicated (that is, bear the most explanatory weight) in the behaviors of networks as systems compared to the vertices (objects) of the multigraph. If so, in this mitigated sense, the behaviors of systems involve “emergent” properties, dependent on how a system is put together rather than of what it is made.³⁰ An example, discussed in some detail by Sarkar (1998: 168–173), is the molecular explanation of dominance which was an ubiquitous feature of classical genetics: why, for some traits, the heterozygote is phenotypically identical to one of the homozygotes. The best explanation so far seems to be in terms of the topology of the reaction networks connecting the DNA specifying the alleles to the molecular structures corresponding to the phenotype. (However, experimentally, the issue is far from settled.)

The relevance of such a situation to structural realism is straightforward: in cases where structure matters more than identity of the parts, it is highly likely that the topology of the network will be resilient across many theory changes involving revisions of the identity of the units (that is, the edge sets will be more resilient than the vertex sets of the multigraph). Moreover, and this point deserves emphasis, such resilience is logically independent of whether there is any more interesting sense in which the networks exhibit emergent behavior. Thus, though this section is on structural emergentism, the emphasis is on structure rather than on emergence. In what follows, to focus on structure, the issue of emergence will be intentionally ignored.

Complex networks of this type constitute the central metaphor of the apparently emerging discipline of systems biology that has become a component of postgenomics. Such complex networks are also supposed to explain ecological behavior—in particular, the emergence of large-scale order—over both large spatial and temporal scales.³¹ Most models of “complex adaptive systems”—yet another popular metaphor of contemporary science—are network models. In fact, to the extent that an alleged science of complexity exists (and there is room for skepticism on this point [Horgan 1995]), it is a science of networks. The relevance to immunology of network models—under the rubric of idiotypic networks (Jerne 1974)—has long been postulated though never fully satisfactorily demonstrated.

Turning to only somewhat less speculative areas, complex gene regulatory networks (GRNs) are supposed to provide, at present, the most viable candidates for understanding organismic developmental

³⁰ This is intended to be a minimalist and neutral epistemological characterization of emergence. For an introduction to the tendentious philosophical disputes regarding this doctrine, see Bedau and Humphreys (2008).

³¹ See, for example, Pascual and Dunne (2006) and Fortuna (2007).

cycles (from germinal cell through the adult stage to reproduction) (Davidson 2006). In this field, they have an illustrious pedigree, going back to Boveri's work at the beginning of the twentieth century, and continuing to what is called developmental evolution today.³² Current GRN models can be traced back to Britten and Davidson's (1969) model which was the first putative general model of eukaryotic gene regulation given the complexities of eukaryotic genome structure that had begun to be recognized in the 1960s. Though there was some formal similarity between this model and the earlier operon model (for prokaryotic gene regulation—see Section 4.1), and textbooks of the period routinely (over)emphasize this aspect³³, unlike the operon model, the Britten-Davidson model was not concerned at all to explain feedback regulation; rather its aim is to explain tissue differentiation and the development of complex form—hence its inclusion in this section rather than in Section 4.1. Though largely ignored for a generation, as the complexity of eukaryotic genetics seemed to defy any modeling strategy (Sarkar 1996), a much-modified Britten-Davidson model and its descendants, in the form of GRNs, have returned to the forefront of research in cell differentiation and organismic development in postgenomics. Whether these models live up to the hopes of their enthusiasts remains to be seen—let me note that, among biologists, there remains ample ground for skepticism.³⁴

From the perspective of this paper, these developments suggest the following conclusion: to the extent that the biological sciences may have any universal mathematical structure (that may potentially play the same unifying role as symmetry groups play in modern physics), that structure seems to be that of directed multigraphs. Perhaps what structural realism should focus on is on the demarcation of the types of directed multigraphs that are relevant for biological theory, and then a classification of these based on the roles they play in various biological sub-disciplines.

4.3. *Developmental Form*

The final set of research programs to be considered here consists of models that have remained speculative throughout their roughly 150-year history. These are macroscopic models (“macroscopic” in the sense that they are concerned with large spatial structures) of developmental form, how organisms produce their adult forms through the history of interactions between the physical contents of germinal cells and their environments. One important class of such models consist of those that rely on details of the physical interactions of the molecular constituents—perhaps the best-known such model was that introduced by

³² Thanks are due to Manfred Laubichler (unpublished work) for providing this history.

³³ See, for example, Lewin (1974).

³⁴ See Newman (2019).

Turing (1952), based on equations for reaction-diffusion systems, and capable of generating a wide variety of spatial forms.³⁵ However, what are most pertinent to the question of the plausibility of structural realism are models that are based on spatial regularities and transformations that are independent of assumptions of the details of the underlying physical interactions. Nineteenth-century morphologists such as Cuvier established several such rules across phylogenetically related sets of taxa in a period when virtually nothing was known about the underlying physical or chemical mechanisms. Embryologists followed their lead by producing similar analyses not only on adult forms but on the developmental stages of organisms generating interesting possibilities, for instance, the hypothesis of the existence of a near-universal phylotypic stage for many animal phyla (Raff 1996).

In the twentieth century, D'Arcy Thompson's (1917) *On Growth and Form* provided a remarkable compendium of mathematical rules that transform spatial features of one taxon to phylogenetically related spatial features of others. Thompson's project involved a shift away from evolution (and history) to questions of form and universal rules that may govern their genesis. For structural realism, what is intriguing is that such mathematical transformation rules would likely be independent of the details of the underlying physical (or chemical) basis and thus be resilient to changes of the ontology of the objects being postulated by models of development. Since the 1980s, with the advent of ubiquitous computation, a further set of models for spatial patterns have been investigated, especially using cellular automata: these models show how very simple generative rules may lead to complex spatial patterns. Beyond organismic development, these rules may also be relevant to the appearance of long-range spatial and temporal patterns in ecology (Ermentrout and Edelstein-Keshet 1993).

Returning to organismic development, what remains unclear, is the *nomological* status of D'Arcy Thompson's and similar transformation rules, whether they are any more than piecemeal (accidental) generalizations that reflect no deep structure of developmental processes. Skeptics of laws of developmental form have ample ammunition on their side: after at least 150 years there is no clear example of a single well-established theoretical law of form. However, whatever be the merit of these hopes, the quest for laws of form seems to continue to find deep resonance in the intuitions of many developmental biologists.³⁶ Arguably, it is even part of what motivates the recent excitement about "developmental evolution" with its goal of explaining much of the structural diversity of organisms on the basis of (presumably physical) rules of variation at the genomic and other levels of organiza-

³⁵ For a history of these developments, see Keller (2002a).

³⁶ They have also impressed some philosophers. For instance, Fodor and Piattelli-Palmarini (2010) base part of their argument against natural selection on the basis of the existence of such laws of form.

tion and with natural selection playing much more mitigated role than in the received view of evolutionary theory.³⁷ What is most salient (in this context) about the project of developmental evolution is that laws of form, under the guise of laws of variation (at the genomic and, possibly, higher levels of organization) are supposed to be more important in explaining organismic (spatial) structure and variation than natural selection—but further analysis of this project is beyond the scope of this paper.

5. A Skeptical Response

It should not go unnoticed that all three organizational examples from Section 4 share a common feature: to varying extents, they express skepticism about the sufficiency of mechanistic explanation in biology, what I have elsewhere defended and called strong reduction (Sarkar 1998; see, also, Weber [2005]).³⁸ This is the idea that the behaviors of wholes, no matter how novel and unexpected they may appear to be, can be explained from the behavior of their (constituent) spatial parts (obviously including the interactions of these parts). Skepticism about this kind of reductionism, as the research programs discussed in Section 4 show, has a long pedigree in the history of biology. As emphasized several times earlier, those who deny this kind of reductionism, but wish to remain within the confines of modern (post 17th century) science, do not presume that there are processes occurring in biological (or, in general, higher structural level) systems that are not occurring in physical (or lower structural level) systems. Rather, it is a claim about explanatory adequacy or, rather, inadequacy. All research programs discussed in Section 4 share this feature.

Now, as I have contended for several decades³⁹, for all the fervor that it often generates, anti-reductionism (and the various associated forms of emergence) are yet to produce viable research programs with tangible content, for instance (but not limited to), predictions at variance with those made by the mundane reductionism that seems to guide almost all experimental research in biology (Weber 2005). In fact, perhaps the only positive contribution of anti-reductionism to biology, but this is an issue not contended by almost all reductionists,⁴⁰ is that reductionism provides no epistemic (or ontic, if one so chooses) warrant for eliminativism, that is, the view that reduced entities (ob-

³⁷ See Wagner (2007) for an entry into this literature.

³⁸ For expository ease, in what follows, I will call this view reductionism without the qualifier “strong.” For other forms of reductionism, see Sarkar (1998) and the encyclopedia article by Brigandt and Love (2008).

³⁹ See Sarkar (1989, 1998, 2008) and Wimsatt and Sarkar (2006). See, also, Weber (2005).

⁴⁰ Almost all, but not all—see Churchland (1986) for a defense of eliminativism about folk psychology with respect to neuroscience. Nagel (1949, 1961) rejected eliminativism and most reductionists have (wisely) followed his lead.

jects or processes/ relations/ structures) should be replaced in scientific discourse by those used to effect the relevant reductions. The claims of this paragraph can be bolstered with plentiful and diverse cases, especially since the advent of molecular biology in the 1950s.⁴¹ Suffice it here to mention two canonical examples relevant to teleological holism and already mentioned in Section 4.1: the allostery model which mechanistically (reductionistically) explained the co-operative behavior of macromolecules (including the Bohr effect for hemoglobin), and the operon model which so explained feedback regulation of gene expression in prokaryotes.⁴² As indicated in Section 4.1, these examples are important because feedback regulation and co-operative phenomena were considered to constitute definitive exemplars of challenges to reductionism from within the anti-reductionist repertoire. Absorbing them within the reductionist agenda does much to deflate the prospects for cogent anti-reductionism.

These observations are pertinent because they help generate a strong presumption that all organizational examples of Section 4 may represent no more than flights of fancy, rich in mystical speculation about the nature and direction of biology, particularly of a future biology which remains indiscernible today, but are nevertheless devoid of empirical content. That is to say, there is no empirical basis for postulating the structures required by the teleological holists, the structural emergentists, or the developmental form theorists. It seems odd to speculate on the persistence or resilience of structures which have no empirical basis today—and worse than odd to draw strong ontological conclusions on those grounds.

Nevertheless, excessive skepticism or criticism of incipient scientific programs is also often misplaced. Take genetics. Returning to a case introduced in Section 2, if Pearson's typically highly cogent biometrical criticisms of the new Mendelism around 1900–1905 had derailed the program of Mendelism initiated by Bateson and, slightly later, Punnett, long before the advent of successful model-building by Haldane, Fisher, and Wright,⁴³ theoretical population genetics may well have not emerged as early as it did or, perhaps, never in the form in which it is now known and provides the basis for evolutionary theory.⁴⁴ It can, therefore, be argued that all three programs—teleological holism, structural emergentism, and developmental form theory—should be treated with tolerance, at least for the time being. Here, tolerance is supposed to mean that such research programs should not be dismissed out of hand, either epistemically (in terms of serious consider-

⁴¹ See Sarkar (1998) and Weber (2005).

⁴² For more details on these examples, see Sarkar (1998).

⁴³ For historical and philosophical details, see Provine (1971), and Sarkar (2004, 2007).

⁴⁴ Obviously, the second disjunct expresses some skepticism about a realist interpretation about even a body of science as empirically well-established as theoretical population genetics. This skepticism is intentional.

ation and active debate) or institutionally (in terms of funding, *etc.*), in the way, say, traditional vitalism or Intelligent Design or other forms of creationism should be so dismissed.

However, in the case of teleological holism, the time for such tolerance may well have long expired. As noted in Section 4.1, this set of claims emerged in their modern form as far back as the late eighteenth century, flourished for a while in the nineteenth century, was given new life by the physiology of the late nineteenth and early twentieth century, and reinvigorated again in the cybernetic era—all this while producing no tangible alternative to the expanding research program of resolute mechanists. The time has come to take stock of these repeated failures rather than wait for promissory notes to be delivered.⁴⁵

Similar pessimism seems also warranted for the search for developmental laws of form. D'Arcy Thompson's *On Growth and Form* continues to provide inspiration to those who seek laws of form, and the aesthetic appeal of the book is denied by few—nevertheless it takes some faith to claim that Thompson's project any longer continues to be a useful resource for biologically-relevant inquiry (and, indeed, probably most historians of biology would now judge that it never did). Let me add that I do have that faith but my position is that of a small minority within developmental biology. To the very limited extent that models in the tradition of Turing (1952) have been successful towards the explanation of biological form, they have done so (as noted in Section 4.3) purely mechanistically, by relying on the physical (and chemical) properties of individual parts rather than mainly on structure independent of constituent details. Recent developments suggest the irrelevance of Turing-type models in contexts where they once appeared most promising, for instance, in explaining segmentation patterns in insects.⁴⁶ There appears at present to be only one prospect that may warrant tempering this pessimism—if the program of developmental evolution succeeds, and does so by explicitly going beyond standard mechanistic (reductionist) models (as, for instance, Laubichler and Wagner [2001] promise), laws of form may well enjoy a new lease of life.

This leaves the case of structural emergentism. As briefly indicated in Section 4.2, but worth special emphasis here (where a more philosophically critical appraisal of this position is being attempted), the issue of emergence is a red herring. In the present context it is not particularly interesting whether there is any interesting sense in which a feature of a system is relevantly different from those of its constituent interacting parts to be deemed emergent. What is at stake is whether in accounting for the feature, what bears the explanatory weight is the structure of the system (as modeled) compared to the identity of

⁴⁵ It is beyond the scope of this paper to assess whether a more positive—or, at least, a less negative—assessment is warranted with respect to the relationship between the mental and the biological. There is a vast philosophical literature to this topic which, fortunately, is not relevant to the topic of this paper.

⁴⁶ See Akam (1989).

the individual parts (objects). A full explication of “explanatory weight” is beyond the scope of this paper. Suffice it here to reduce it to the question whether the explanation can be extended to a large variety of other systems that have the same structure but differ in the constituent objects: the greater the differences between the sets of objects, the greater the extent to which the structure, rather than the objects, bears the explanatory weight.

The molecular explanation of dominance (which was alluded to in Section 4.2) may be one exemplar of this possibility. However, it may well be an isolated case given that no other such case seems to have been offered in the philosophical literature since Sarkar (1998) analyzed the case of dominance. Moreover, it is hard to be generally optimistic about the prospects of GRN models or any of the other kinds of network models that dominate the bulk of theoretical biology today. However, in the case of GRN models, it is too early to be sure of their eventual fate but this should surely be regarded as a situation in which excessive skepticism about an incipient research program is unwarranted. Nevertheless, all that there is at present is a promissory note.

6. *Final Remarks*

Where does this leave us? I wish to make five observations:

1. Structural realists have a wealth of evidence on their side drawn from the history of science in support of the claim that theoretical structures (for instance, relations between putative objects) are far more resilient than theoretical objects across radical theory change. This assessment is not limited to the biological contexts with which this paper is concerned. A large array of studies by (both epistemic and ontic) structural realists provide support for it from the physical sciences (Ladyman and Ross 2007).
2. Though laws (a particular type of structure) do enjoy this kind of preferential resilience compared to theoretical objects, at least in biological contexts they appear to do so only to the extent that they are phenomenological (Section 3). Moreover, even the most resilient phenomenological laws in biology do not show the degree of resilience that would warrant confidence in claims of realism about them. Section 3 showed this to be very likely in the case of the Law of Ancestral Heredity. The status of the Price equation is unlikely to be different though the verdict is still out—and will not be settled in the foreseeable future.
3. What are more likely to have the required resilience—that is, resilience not reducible to being phenomenological—are constitutive frameworks in which a variety of laws can be formulated. Recall the discussion of the Price equation in Section 3: to the extent that it seems to exhibit a high degree of resilience, it is

due to its being more akin to a constitutive framework rather than an individual law.

4. However, there is no reason to suppose that entire frameworks (including those that are at the highest level of generality as explicated in Point 3 above) may never be entirely replaced. What is troubling is that neither French (2011, 2012) nor any other structural realist seems to offer arguments to the contrary.
5. Section 4 noted that directed multigraphs may provide an appropriate constitutive framework for much of theoretical biology. Now, directed multigraphs are mathematical structures at such a high level of formal abstraction that it is important to show that the claim being made here about them is not entirely vacuous (similar, for instance, to a claim that real and complex fields [in the algebraic sense] provide a constitutive framework for physics). There are at least two restrictions that the choice of directed graphs immediately imposes: (i) Somewhat trivially, the relevant structures must exhibit some asymmetry between units (vertices) in their interactions which is represented by the directions of connecting edges. (ii) Far more importantly, directed graphs are discrete mathematical structures. Both restrictions carry over to directed multigraphs. Thus, adopting a framework of directed multigraphs assumes that biological models must be so constructed that the putative objects and relationships between them can be individuated into distinct sets. This excludes for instance, modeling organismic development using what used to be called morphogenetic fields, or in the way envisioned by Turing and those who followed his tradition. This means that claiming that the appropriate structures are directed multigraphs is a claim with non-trivial empirical consequences. It remains an open question whether it is correct and, if so, what other restrictions can be imposed on that structure while retaining its aim of representing as much of biological phenomena as possible.

These observations may not be much in the way of a conclusion. So, I will finally end by claiming something more definite. To the extent that this paper has defended anything at all, it has defended the importance of theoretical structures as opposed to theoretical objects. This amounts to an endorsement of *structuralism* as, for instance, explicated long ago in a mathematical context by the Bourbaki group. But it does not take any position on realism. A quote from Stein (1989: 57) is particularly relevant: “[O]ur science comes closest to comprehending the ‘real’, not in its account of ‘substances’ and their kinds, but in its account of the ‘Forms’ which phenomena ‘imitate’ (for ‘Forms’ read ‘theoretical structures’, for ‘imitate’, ‘are represented by’).” Ladyman and Ross (2007) take Stein to be sympathetic to structural realism. Arguing

against the structural realists, Stanford (2006) takes Stein (1989) to be defending a sophisticated instrumentalism. Neither of these interpretations appears to be fully accurate though Stanford's come closer (notice Stein's careful qualification "comes closest to" before any reference to the "real").

But the deeper point that Stein is making is one I would endorse and extend. Structural characterizations provide resilience against radical theory change. In particular, empirically successful phenomenological laws, interpreted as structures, not only often survive such changes but constrain the form of revised theories by being part of the data that must be accommodated. In general, these structures not only permit persistently corrected predictions (and the use of this ability for technological and other purposes) but, even as they change, they provide better representations of the world in the sense that they are resources for further enquiry that enable the extension of individual sciences and, often enough, their iterative unification. Now, what does the claim "these structures are real" or "these structures are all that can be known" add? Almost certainly, something psychological, especially for those whom James would call tender-minded (as opposed to those who are tough-minded empiricists). But it does not add anything of philosophical significance. Like Stein (1989: 65), we should maintain: realism, "yes"; but instrumentalism, "yes, also"; no only to anti-realism—with anti-realism including not only constructive empiricism but, especially, social constructivism and the other various fashionable forms of relativism that have unfortunately come to dominate much of the history of science in recent decades.

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