UNIFICATORY EXPLANATION

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Abstract

Philosophers have traditionally addressed the issue of scientific unification in terms of theoretical reduction. Reductive models, however, cannot explain the occurrence of unification in areas of science where successful reductions are hard to find. The goal of this essay is to analyze a concrete example of integration in biology—the developmental synthesis—and to generalize it into a model of scientific unification, according to which two fields are in the process of being unified when they become explanatorily relevant for each other. I conclude by suggesting that this methodological conception of unity, which is independent of the debate on the metaphysical foundations of science, is closely connected to the notion of interdisciplinarity.

Contents

1 Introduction

Philosophers have traditionally addressed the issue of scientific unification in terms of theoretical reduction. Simply put, the general assumption was that two scientific theories can said to be unified when one is successfully reduced to the other, or both are subsumed under a broader, more general theory. To be sure, a precise formulation of the conditions for reduction and whether these conditions hold are important problems that spurred lengthy debates. However, for a long time the unity of science was treated—more or less explicitly—as a matter of logical relations between the terms and laws of various branches of science (Carnap [1938]), to be achieved through a series of inter-theoretic reductions (Oppenheim and Putnam [1958]).

Biology constitutes a notoriously challenging terrain for reduction and, consequently, for reductive unification. Whether we adopt the classic framework of Nagel ([1961])—according to which a theory A is reduced to a theory B if and only if the laws of A can be derived from the laws of B by means of bridge principles—or less demanding accounts (e.g., Schaffner [1967]), concrete examples of successful theoretical reductions in the life sciences are scarce. Hence, traditional reductive models of unification leave us facing a dilemma. If reduction is necessary and sufficient for unification, then we ought to conclude that in areas of science such as biology, where there virtually is no theoretical reduction, there is no unification. This conclusion, however, flies in the face of the many scientists, philosophers, and historians who have celebrated the so-called *modern synthesis* of genetics and evolution (Mayr and Provine [1980]) and, more recently, the *developmental synthesis* of evolutionary and developmental biology (Carroll [2005]). A more promising alternative is to reject the assumption that theory reduction constitutes the appropriate framework to assess real or alleged cases of scientific unification. Indeed, the increasing philosophical interest in the special sciences as an independent object of study spurred the development of various non-reductive models that purport to account for how scientific fields can be unified, synthesized, or integrated without thereby being replaced or reduced to one another.[1] Nonetheless, fundamental issues remain unresolved.

The aim of this essay is to sketch a general account of the unity of science modeled on a concrete example from biology. I begin with a brief review of familiar shortcomings of theory reduction, which will provide some guidelines for moving forward. Next, I consider some existing approaches to non-reductive unification and expose some limitations in failing to satisfy important desiderata. The rest of the article is devoted to drawing more systematic relations between explanation and unification, using evolutionary developmental biology as a case study. I conclude by suggesting that the methodological conception of unity developed here is closely connected to the notion of *interdisciplinarity*.

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[1] Alternative conceptions of unification were already considered—but swiftly dismissed—by philosophers of science working within the framework of logical empiricism (e.g., Oppenheim and Putnam [1958]). A notable exception is Neurath, who developed a non-reductive approach to scientific unification as the practice of bringing together researchers working in different fields to facilitate unification and interconnection (Cat et al. [1996]; Potochnik [2011]).

Before we begin, a note about terminology. Historically, *unity* and *synthesis* have often been treated as distinct concepts (Kant is a noteworthy example) and contemporary authors continue to draw scope distinctions between the two terms. In developing my approach to unification, I shall honor this longstanding tradition, employing 'unity' to refer to a broader—perhaps even global—state of science, while reserving 'synthesis' for domain-specific connections between two disciplines (e.g., psychology and neuroscience), and 'integration' for even more localized problem-specific or question-specific connections.

2 Some Troubles with Theory Reduction

Classic formulations of reduction presuppose a conception of theories as consisting of collections of statements, which must include both empirical laws and testable conclusions deriving from them. The inadequacy of this 'syntactic' account of theories—a legacy of logical empiricism—is especially evident in the special sciences. Restricting our attention to biology, the complex structure of cytology, genetics, and biochemistry (Kitcher [1984]) or evolution (Kitcher [1985]) is hard to capture in terms of laws or law-like statements, on pain of trivializing it or generating a dramatically impoverished reconstruction. There are two natural ways of responding to this problem. One solution is to revise the definition of 'scientific theory,' for example, by replacing the syntactic conception with a semantic approach that identifies theories with collections of models (Suppes [1960]; van Fraassen [1980]; Lloyd [1988]). Alternatively, one could deny that genetics, biochemistry, and evolution count as 'theories' at all and replace the term with an altogether different concept, such as Kuhn's *paradigms*, Toulmin's *disciplines*, Laudan's *research programs*, or Shapere's *fields*. Whether biological subfields are better defined as 'theories' or as something else is an important question that, however, I shall set aside. The relevant point, for present purposes, is that the special sciences cannot be adequately captured and described in terms of interpreted axiomatic systems.

Independently of the shortcomings of the syntactic conception of theories, derivational reduction also seems inadequate as a characterization of actual scientific practice. As noted by Fodor ([1974]), the proliferation of new scientific fields is much more common than their merge and reduction. Moreover, perhaps with the exception of a few hackneyed examples—such as thermodynamics and statistical mechanics[2]—genuine instances of theory reduction are hard to come by. The situation is especially troublesome in the context of biology, where even the best candidates for Nagelian reduction, such as Mendelian genetics and molecular biology, notoriously fail (Hull [1974]; Kitcher [1984]). Finally, not only is derivational reduction descriptively inaccurate; even its normative significance as a scientific goal has been seriously questioned (Maull [1977]).

In sum, classic theoretical reduction has fallen on both fronts. The traditional syntactic conception of theories is drastically limited in scope and derivational reduction lacks both normative and descriptive force. Now, surely, *reduc-*

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[2] But see Sklar ([1993]) for some difficulties and qualifications

tionism is still a widely discussed topic and, even in the philosophy of biology and the philosophy of mind, where a general antireductionist consensus reigns, the reductive stance has feisty defenders (Waters [1990]; Bickle [2003]; Rosenberg [2006]). Yet, contemporary reductionism has assumed a different form: current debates largely focus on epistemic issues, such as whether 'higher-level' events can be explained at a more fundamental level, not on attempts to logically derive the laws of one area of science to the principles of another. Similarly, recent attempts to undercut multiple-realization arguments (Sober [1999]; Shapiro [2000]) do not advocate a return to derivational reduction. Theory reduction, at least in the traditional guise, has been beaten to death.[3]

3 Interfield and Mechanistic Unification

The considerations advanced in the previous section raise a specific problem: if reduction is neither necessary nor sufficient for unification, then what does it mean for two branches of science to be 'unified'? This question can be divided in two parts, which should be addressed independently. First, what kind of non-reductive relations connect scientific disciplines? Second, do these relations provide viable alternative criteria of unification?

A good place to start examining non-reductive relations are *interfield theories*—general accounts that conceptualize non-mutually-exclusive relations between scientific fields (Darden and Maull [1977]). In explicit opposition to the syntactic approach outlined above, Darden and Maull characterize 'fields' as areas of science defined by common problems, methods, and techniques. The guiding idea is that theories (or collections of theories) belonging to different fields often do not compete and cannot be logically reduced to one another; nonetheless, fields and theories therein may be connected in various ways. As an illustration, consider how the existence of Mendelian factors, their relevance for heredity, and even their relation to chromosomes was already postulated by classical geneticists. What classical genetics lacked were the conceptual and experimental resources to determine the molecular structure and function of genes and to explain causally the process of heredity. It was only with the advent of molecular biology and biochemistry that the chromosomal location of genes, their double-helical structure, their role as protein templates, and many other details of gene expression were finally uncovered. This goes to show how new fields often specify the location, structure, function, and causal relevance of entities and processes posited in a different discipline, confirming previous findings, generating new predictions, and coordinating future research. It should be evident that none of these relations is 'reductive'; even once the relevant interconnections are made explicit, classical genetics and cytology remain largely

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[3] Various authors have recently attempted to rehabilitate Nagelian reduction by providing an epistemic interpretation of his *condition of connectability* (Fazekas [2009]; Klein [2009]). The prospects of salvaging Nagel's model pose an interesting question, albeit one that I shall not address directly. Epistemic approaches to unification are discussed in §3; my point so far is that *derivational* reduction fails to capture the complex structure of the special sciences.

independent and distinct. Still, the resulting interfield theory—the chromosome theory of Mendelian heredity—effectively integrated the two disciplines, without replacing or reducing one another, by bringing together knowledge of heredity and thereby explaining the analogous properties of chromosomes and genes.

Darden and Maull's proposal has been developed in various ways. For instance, the idea that a new field can illuminate the foundations of a prior theory and extend the range of possible explananda was further elaborated by Kitcher ([1984]) in terms of 'conceptual refinements' and 'explanatory extensions.' The core insight is that scientists often postulate entities whose structure and function are not yet fully understood, and formulate questions that cannot be answered by the concepts and technologies presently available in their fields. When this happens, the relevant explanations can sometimes be found in a neighboring discipline. If theory T^* provides an illuminating description of entities that fall within the domain of theory T, Kitcher says, T^* provides a *conceptual refinement* of T. Similarly, when T^* sheds light on some schematic premise of a problem-solving pattern in T, T^* is an *explanatory extension* of T. In the above example, molecular genetics constitutes both a conceptual refinement and an explanatory extension of Mendelian genetics, as the former uncovered the structure of genes and genetic processes, which figured as crucial postulates in the latter.

More recently, other authors have substantially broadened the range of interfield connections originally considered by Darden and Maull. Kincaid ([1990]) individuates seven kinds of inter-theoretic relations, including *overlapping ontologies*, *logical compatibility*, two kinds of *supervenience*, *heuristic dependency*, *'confirmation' dependency*, and *shared explanations.* While the list is not meant to be exhaustive, when all these requirements are met, Kincaid says, unity reaches its pinnacle and the two theories are incorporated into an *integrated interlevel theory.* Grantham ([2004]) recognizes a similar array of connections, and classifies them into two categories: *theoretical interconnections*, which involve conceptual, ontological, and explanatory relations, and *practical interconnections*, which involve relations of heuristic dependence, confirmational dependence, and methodological integration. Recent work in data-integration can be interpreted in a similar light, as an attempt to broaden the kinds of relations that can be established among fields (O'Malley and Soyer [2012]; Leonelli [2013]).

Influential as they are, interfield approaches are not the only response to reductive unification; the surge of the so-called 'new mechanistic philosophy' also provided an alternative framework for conceptualizing non-reductive relations between areas of science. In ongoing work spanning almost three decades, Bechtel ([1986; 2006]) has advocated a shift in philosophical theorizing, according to which progress and change in experimental biology should be analyzed in terms of mechanistic explanation. An analogous approach has also been adopted by Darden herself who, in later work, reformulated her own concept of interfield theory within a mechanistic framework (Darden [2006]). On this interpretation, the structure of biological subfields is understood not as sets of laws or theories, but through an appeal to *mechanism schemas.* Scientific progress and integration, she now argues, occur through a progressive discovery of separate-but-serially-connected mechanisms with working entities of various sizes, which are gradually filled in with more specific descriptions of components and activities. Similar analyses have also been offered by other authors associated with this mechanistic philosophy, who argue that fields are integrated via the addition of constraints to the organization of mechanisms (Craver [2007]; Baetu [2011]; Craver and Darden [2013]).

In sum, one can identify and analyze a variety of relations between fields. With them in mind, we can move on to the second question: whether these models provide a viable model of non-reductive unification. Interfield and mechanistic accounts provide illuminating descriptions of scientific practice and progress. Yet, I contend, both approaches leave two fundamental issues unresolved.

The first problem is that most extant accounts lack normative force. Even conceding that interfield and mechanistic models accurately *describe* the practice of scientific unification, they fail to *explain* why unification is (or should be) an important scientific endeavor. To appreciate this point, it is instructive to compare contemporary approaches with the classic reductive framework. Oppenheim and Putnam's 'unity of science as a working hypothesis' purported to offer more than a description of an alleged trend. In addition, it captured an important epistemic goal: scientists should attempt to reduce (i.e., unify) theories because science has a single and coherent metaphysical foundation and, consequently, unification is a way of furthering scientific progress. This reductive picture of science as globally and fundamentally unified, however, has been challenged both as a suitable foundation and as an attainable goal. For one thing, the observation that '[t]he development of science has witnessed the proliferation of specialized disciplines at least as often as it has witnessed their reduction to physics' (Fodor [1974], p. 97) undermined straightforward historical metainductive arguments purporting to establish unity as an actual trend. Members of the so-called 'Stanford School' have challenged the view even more radically, by advancing an opposing metaphysics according to which science is fundamentally 'disunified' (Dupré [1993]; Galison [1996]; Hacking [1996]; Cartwright [1999]). In the absence of a 'layer cake' hierarchical model of sciences resting on a monolithic foundation, one cannot simply assume that unification furthers progress. Describing the unification process is thus important, albeit insufficient: the ideal of a unified science cannot be taken for granted; it requires independent justification.

We shall return to the significance of unification for the advancement of science in §5 below. For the moment, let us consider a different problem: extant interfield and mechanistic accounts are of little use for assessing the various stages and degrees of the unification process. First, consider Kincaid and Grantham's proposals, where the kinds of interconnections are formulated more explicitly than in the original account. Taken as a whole, their sets of inter-theoretic relations constitute a plausible upper bound for unification: when all conditions are satisfied, fields are connected by an integrated interlevel theory and unification reaches its pinnacle. But does unification also have a *lower bound*? Can we conclude that fields are minimally unified (or in the process of being unified) when they satisfy some but not all conditions? If so, which ones? Treating *all* conditions as necessary is too demanding, as fields can be unified without, for example, exhausting each other's ontologies—genes postulated in molecular biology are arguably different entities from genes in Mendelian and population genetics (Dupré [1993]). At the same time, treating *any* subset of conditions as sufficient for unification is too weak. The definitive rejection of vitalism suggested an uncontroversial sense in which biology supervenes on physics: all organisms are composed of atomic and subatomic particles subject to physical laws. Yet, it would be preposterous to maintain, on these grounds alone, that biology and physics are (being) unified. Likewise, the logical consistency of theories is a plausible necessary condition for unification, but it is hardly a sufficient one. Similar considerations apply, *mutatis mutandis*, to mechanistic models: even granting that the unification of classical genetics and cell biology is the result of a serial integration of mechanism schemas, at what stage did the synthesis begin? Which mechanism schema marks the transition to the integration stages?

In conclusion, a general account of scientific unification must fulfil, among other things, two independent desiderata. First, it needs to motivate the significance of unification for scientific progress. Second, it should provide some general criteria for identifying the various stages of a synthesis and comparing degrees of unification across areas of science. Extant models models fail to satisfy either condition. In an attempt to begin articulating an alternative that meets these standards, in the following section, I examine an ongoing integration in biology: the developmental synthesis.

4 Foundations of the Developmental Synthesis

The last few decades of the 20^{th} century have witnessed the emergence of a new branch of the life sciences, called *evolutionary developmental biology* ('evo-devo,' for short), which aims at bridging the methodological and theoretical gap that has separated development and evolution since the early 1900s. It attempts to do so by uncovering the molecular processes and developmental trajectories by which modifications of gene regulation processes trigger and constrain phenotypic variation, originate in evolutionary novelties, and alter body plans. A general overview of the massive evo-devo literature is clearly besides our purposes. The questions that I shall address here are: what do researchers mean when they claim that a 'synthesis' of developmental and evolutionary biology is currently in progress? And what evidence do we have in support of the thesis that these fields are finally being (re)unified?

The significance of these questions can be motivated by two independent reasons. The first is exquisitely philosophical. The relationship between development and evolution cannot be framed in terms of theoretical reduction, for the complex structure of these fields resists being captured as interpreted axiomatic systems and, no matter how loosely we interpret 'reduction,' they are not being reduced to one another. Hence, the so-called developmental synthesis provides a good case study for non-reductive models of unification. The second reason for focusing on evo-devo transcends purely philosophical reflection and cuts deep into scientific research. In spite of fairly widespread (but by no means unanimous) agreement on the ongoing unification, a broad consensus on the nature of the developmental synthesis is yet to be achieved. Researchers coming from a wide variety of biological and philosophical traditions are united under the aegis of evo-devo, turning this newborn field into a hodgepodge of goals, methodologies, and projects.[4] Consequently, the precise relation between evo and devo is often left unspecified, or described with general, undefined blanket terms such as 'synthesis' or 'integration.' In short, clarifying the nature of the developmental synthesis is an important philosophical and scientific endeavor, furthering the achievement of a unitary methodological perspective.

So, in what sense are development and evolution being synthesized? To begin, we should note that biologists have been aware of their mutual relevance at least since Darwin and Wallace, the founders of modern evolutionary theory, who speculated that bringing to light the mechanisms of development is the key to understanding evolution. The co-dependence of the two fields was eventually crystallized in Haeckel's (in)famous biogenetic law: 'ontogeny recapitulates phylogeny' (Gould [1977]). However, it was only with the advent and progress of molecular biology, in the second half of the 20^{th} century, that the nature of developmental processes began to be uncovered. Up to that point, the mechanisms of ontogeny had to be set aside and 'black boxed': their presence was indisputable, but their precise identity and structure was—and to a great extent still is—beyond our ken. Next, consider the relation between the two fields. Given that the evolutionary trajectory of a population supervenes on the development of its members, the mechanisms of ontogeny constrain and (partially) determine phylogeny. Is this fact alone sufficient to ground unification? Many scholars, more or less explicitly, suggest that it is. According to a widespread view, the developmental synthesis constitutes an attempt to close the gap left open by the founders of the modern synthesis. Evo-devo addresses a fundamental issue that was once black-boxed and set aside: the nature and structure of the mechanisms responsible for turning genetic mutations into changes at the phenotypic level (Carroll [2005]).

The problem with this view is that bridging an explanatory gap, no matter how significant, is insufficient to warrant a *synthesis*. To illustrate, consider one of the central goals of evo-devo: the discovery and explanation of *evolutionary novelties*, that is, qualitatively new morphological structures found in a population of organisms but not in an ancestral one, such as vertebrate jaws or avian feathers. Brigandt ([2010]) argues that uncovering the nature of evolvability requires the integration of different disciplines, such as genetics, developmental biology, morphology, phylogeny, as well as paleontology, ecology, and biogeog-

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[4] Symptomatic of this variety of perspectives is Hall's ([2000]) distinction between *evo-devo*, a synthesis of evolution and development, and *devo-evo*, a new form of developmental evolutionary biology purporting to modify or even replace the Modern Synthesis. As Hall argues, transforming development in the light of evolution or vice versa would yield different results.

raphy.[5] However, as Brigandt notes, the evo-devo concept of *novelty*—a new structure that is non-homologous to ancestral traits—is quite different from the corresponding neo-Darwinian notion, intended as a change of function in an existing structure. This discrepancy in explananda is a particular instance of a more general phenomenon: the discovery of ontogenetic mechanisms is a task that lies beyond the scope of evolutionary theory and genetics, as traditionally conceived (Amundson [2005]). Without downplaying a remarkable scientific achievement, the point is that this finding, by itself, falls short of a *bona fide* integration. Given that both classical genetics and Darwinian evolution *assumed* (but did not attempt to explain) the mechanisms of variation, it is hardly surprising that the modern synthesis remained moot on this important point. But then, if evo-devo is addressing a problem that falls outside the domain of one integranda, how is it a 'synthesis'?

The upshot is that bringing a field to address fundamental questions that are assumed—but left unexplained—by another field is insufficient to ground a synthesis. Supervenience and explanatory extension, even when combined, fall short of genuine unification. From these observations, one might be tempted to conclude that evo-devo is not really a full-fledged synthesis, after all, but a strictly local integration aimed towards the solution of specific problems—an approach that is becoming increasingly popular among philosophers of biology, including Brigandt himself. A less radical conclusion, however, can be reached by adopting a different account of unification. In the rest of this section, I argue that what lies at the heart of the developmental synthesis is *explanatory relevance*. What warrants the assertion that development and evolution are in the process of being unified is that ontogenetic concepts are required by certain phylogenetic explanations and, conversely, some developmental explanations presuppose an evolutionary framework.

To motivate my thesis, let us consider some of the scientific breakthroughs that underlie the developmental synthesis. The aspirations of evo-devo stem from groundbreaking biological findings, such as remarkable analogies in the development of flies, mice, humans, elephants, and other organisms that are loosely related from a phylogenetic perspective. More specifically, the staggering discovery was that virtually all multicellular organisms employ the same accurately-conserved 'genetic toolkit,' which organizes developmental pathways across a variety of clades—a feature of ontogeny that is typically referred to as *molecular parsimony*. This opened up phylogenetic questions that could not be addressed with the standard concepts and methodology of evolutionary theory and, at the same time, emphasized the importance of embedding developmental processes within an evolutionary framework. Consequently, an integrative set of concepts and tools became necessary to address these new explananda.

To narrow the focus of the discussion, let us consider a concrete example. *Hox* genes are a subset of master control genes that govern the *Bauplan* of developing organisms. The significance of *Hox* genes for development is hard

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[5] For a systematic analysis of the multidisciplinary nature of the explanation of evolutionary novelties and innovations, see also Love ([2008]) and Love and Lugar ([2013]).

to overstate, as these genes are responsible for the specification of the identity and structure of entire anatomical segments and functional traits. For instance, whether a particular segment of a fruit fly develops into a haltere, a wing, an antenna, or a leg is determined by the pattern of expression of the *Hox* genes in the segment in question.[6] In a more metaphorical fashion, we may compare the development of an organism to a construction site where an embryo is 'built.' While structural genes code for proteins, which correspond to bricks and other basic blocks, master control genes play a functional role that is analogous to a master plan, the instructions that determine how the various blocks combine to form the embryo. Just as substituting a building plan can turn a skyscraper into a townhouse, *Hox* gene mutations may transform the identity of a trait, so that one finds flies with legs instead of antennas stemming from the forehead or with an abnormal number of wings.[7]

Setting the obvious developmental significance of *Hox* genes aside, where does evolution come into the picture? Genetic and molecular similarities within and across species raise specific questions which can only be addressed by integrating the ontogenetic framework with evolutionary concepts. Consider, first, *intraspecific* similarities, such as the ubiquity of the homeobox sequence, which is found in all *Hox* genes, regardless of the timing and location of their expression. Molecular parsimony raises deep and puzzling issues: why are the same molecules and mechanisms employed in completely different and independent parts of the embryo? These questions have evolutionary answers. Borrowing a somewhat technical term, *Hox* genes are *paralogous*: they all derive from the duplication of an ancestral gene. In other words, the specialized master control genes that govern the development of each body part were not created from scratch; they all evolved from a single ancestor through several rounds of duplication and random mutation, during which they acquired the new functions and specializations underlying phenotypic diversity. To be sure, appealing to paralogy, by itself, does not provide a complete explanation of phenotypic development. However—and this is the crucial point—the evolutionary concept of paralogy provides the general framework in which the developmental explanation can be spelled out: it is the evolutionary history of the trait that explains the presence of the same genetic sequence in various kinds of specialized cells.

Analogous considerations apply to *interspecific* similarities, such as the conservation of nucleotide sequences across species. As noted, the homeobox is uni-

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[6] Clearly, the presence or activation of genes alone is not sufficient for the development of a trait, in the absence of the entire ontogenetic apparatus and relevant environmental conditions. The point is that these genes are difference-makers that determine the identity of segments in physiologically 'normal' organisms, developing in 'appropriate' conditions (Nathan [2012]).

[7] In order to understand how master genes are able to perform this crucial role in development we need to take a deeper look into their molecular structure. All *Hox* genes across organisms and species have in common a short (approximately 180 base pairs) stretch of DNA—called the *homeobox*—that encodes a protein domain, known as the *homeodomain*. Proteins in the homeodomain are transcription factors, that is, molecules that bind to DNA sites to enhance or inhibit the transcription of genes. These proteins have a regulatory function: they specify the identity of body segments by activating the genes required to build particular traits.

versal: virtually all multicellular organisms have *Hox*-like genes.[8] This raises an obvious question: why do flies, elephants, humans, and other organisms which are quite distant from each other from both a phenotypic and a phylogenetic perspective employ the same genetic sequences in their development? Again, analyzing the problem from an evolutionary perspective suggests a straightforward answer. The widespread diffusion of the homeobox is explained by *Hox* genes being *orthologous*, that is, homologous across species: all *Hox* genes were inherited from a common ancestor and subsequently modified through mutations and duplication events. In sum, evolutionary concepts such as homology are necessary to explain analogies and differences in developmental processes across organisms and species, and even between different parts of the same organism.

Before moving on, two important clarifications are in order. First, it should be obvious that, while I have focused on *Hox* genes, similar considerations apply to other classes of genes or even to larger developmental units. For instance, the *theory of facilitated variation* (Kirschner and Gerhart [2005]; Gerhart and Kirschner [2007]) appeals to core processes that, just like master control genes, are conserved within and across organisms and, in addition, provide an account of how these core processes can be reused and rearranged to generate evolutionary novelty. A comprehensive discussion of the connection between genes and phenotypes clearly transcend our present purposes. Still, it is worth noting that broadening the scope of the discussion of core processes at the genetic level to include examples at the cellular level (and above) facilitates the connection from molecular structures to morphological phenotypes, thus providing a better explanation of *evolvability*—the generation of novel and functional phenotypic variation—which is another important aim of evo-devo.

Second, some readers may worry that the above 'developmental questions' are really evolutionary problems in disguise.[9] Evolutionary concepts such as paralogy and orthology are indeed required for explaining how different traits, organisms, or species came to develop in various ways. However, the objection runs, these are not problems for *developmental* biology, but for *comparative* developmental biology, a discipline that falls under the broad umbrella of phylogeny, comparative biology, or evolution. Hence, the need for an integrated framework is only apparent: once 'evolutionary' (*sensu lato*) and developmental problems are appropriately classified, their independence becomes evident. This objection raises an important—albeit thorny—issue regarding the individuation of biological disciplines. Clearly, if one restricts developmental explanantia to a mechanistic description of the processes taking place during the ontogeny of individual organisms, evolution cannot play a role in the explana-

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[8] What makes these similarities stunning is the degree of conservation of the signature sequence (McGinnis et al. [1984]). For instance, sequence of amino acids in the homeodomain proteins of mice and frogs are identical at up to 59 out of 60 positions, despite the fact that the evolutionary ancestors of these species diverged over 500 million years ago, before the famous 'Cambrian explosion' that gave rise to most animal types. In addition, these remarkable interspecific similarities transcend the sequences of nucleotides, extending to the arrangement of genes into clusters on the chromosomes and their patterns of extension.

[9] I am grateful to an anonymous reviewer for raising this objection cogently, bringing my attention to the theory of facilitated variation, and drawing the connection with evolvability.

tion. It does not follow, however, that evolution has nothing to contribute to the study of development, more broadly construed. The main role of evolution within developmental studies is to raise some novel questions and to show how such questions can be answered via an integrative framework. Suppose, for example, that one had a satisfactory mechanistic account of the processes underlying the development of the wings and antennas of a fruit fly, and noted some remarkable similarities between the two descriptions. Can we explain why these processes are so similar, given the myriad possible ways in which these traits could develop? Note that this question does not count as 'developmental,' on the narrow definition provided above, as answering it requires more than a mechanistic description of the process at hand. However, strictly speaking, the question is not an exquisitely 'evolutionary' one either, as addressing it requires more than the evolutionary history of the trait. The similarity between the two developmental mechanisms is a hybrid explanandum with a hybrid explanans: the solution presupposes both a mechanistic description of the process in question and a specification of phylogenetic details. Someone pressing the above objection might well insist that developmental biology is not (and should not be) in the business of providing such hybrid explanations. If that is the case, then evolution has nothing to contribute to developmental biology, thus narrowly defined. However, the important point remains that the integration of development and evolution can raise and address significant problems about the ontogeny and development of organisms. Indeed, as noted by prominent biologists 'you cannot understand anything about development without understanding evolution' (Walter and Gehring [2002], p. 36).

Just as the study of ontogeny requires an evolutionary framework, developmental concepts are also essential in evolutionary biology. An area of contemporary evolution in which ontogeny plays an indispensable explanatory role is the study of *developmental constraints*—biases in the production of variant phenotypes or limitations of phenotypic variability caused by the structure, character, composition, and dynamics of the developmental systems (Maynard Smith et al. [1985])—which limit the variation in form and body plan by preventing the evolution of populations from following certain trajectories and bias it in favor of others. The idea that developmental constraints provide a bridge between ontogeny and phylogeny is of old vintage, going back at least to T.H. Huxley and, later, to Vavilov's 'law of homologous variation.' Yet, it is only in the last decades of the 20^{th} century that this idea became central to biology, sparked by two seminal articles: Jacob's ([1977]) model of evolution as 'tinkering' with the resources available at a particular place and time, and Gould and Lewontin's ([1979]) trenchant critique of the adaptationist program. Both articles essentially argue that viewing natural selection as fundamentally independent of development is highly misleading; the moulding force of evolution on a population cannot be meaningfully separated from the developmental forces that shape individual organisms. As a result, adaptive explanations that treat each phenotypic trait as independently engineered by evolution, and developmental studies that overlook the optimizing action of natural selection, are equally bound to misunderstand biological processes. The pervasiveness of the homeobox throughout the animal kingdom suggests precisely that there are certain kinds of perturbations that nature just cannot make. Any substantial tinkering with homeoboxes and other regulatory sequences in master control genes is more than likely to produce nonviable organisms.

5 Explanatory Relevance

Let us take stock. This essay began with a review of some well-known problems with reductive unification, followed by a discussion of alternative accounts that purport to capture how fields can be interconnected without being thereby replaced or reduced to one another. While interfield and mechanistic models constitute an improvement over traditional reductive ones, I argued that they still fall short of a satisfactory account of scientific unification. The examination of evo-devo suggested that what underlies the developmental synthesis is the explanatory relevance of ontogeny and phylogeny: evolutionary and developmental studies are mutually enriched and extended by the integration of developmental concepts and the evolutionary framework. These considerations can be moulded into a general criterion for scientific unification.

(ER) Two fields A and B are in the process of being unified when (and only when) they are explanatorily relevant to each other, that is, when conceptual advancements and testable results in A are necessary for raising explananda and providing explanantia in B and, vice versa, results from B are required to pose and address questions in A.

The connection between unification and explanation is of old vintage, figuring prominently both in theories of explanation (Friedman [1974]; Kitcher [1981]) and, more or less explicitly, in all accounts of unification discussed above. I should thus clarify how the view advanced here differs from existing proposals. My contention is that, of the various interconnections postulated by interfield theories, a single one—explanatory relevance—lies at the core of unifications, of both theoretical and practical ilk. Specifically, my claim is that *explanatory relevance is both necessary and sufficient for unification.* Let us focus on the necessity claim first. As noted above, logical compatibility, by itself, is too weak to warrant even a small degree of unification. However, it does further unification when coupled with explanatory relevance, for instance, when we have multiple competing evolutionary hypotheses, only one of which is consistent with developmental results. Similarly, the supervenience of a discipline over another or a shared ontology only further unification when backed up by explanatory relevance; otherwise, a modest token physicalism would be sufficient to ground the unification of, say, physics and economics. Finally, since the demise of logical empiricism, claims about heuristics and confirmation are generally relativized to specific explanatory contexts. In a nutshell, explanatory relevance lies at the very core of scientific unification. To be sure, the claim is not that all other relations are inaccurate or insignificant. My suggestion is rather that their role in unification is grounded in, motivated by and, ultimately, reducible to their contribution to the explanatory relevance of fields.

Next, let us examine the sufficiency claim. There are two different lines of objection that might be pursued here. First, one might be concerned that explanation is not broad enough to capture all forms of unification. Perhaps, one can make sense of the developmental synthesis in terms of explanatory relevance, but what about fields like engineering and biology—which are integrated in biomedical engineering, systems biology, and synthetic biology—where explanatory relevance requires and presupposes the development of new concepts and methods that are applicable in new fields? In such cases, what does the unificatory heavy lifting, the objection runs, is conceptual and methodological integration, not explanatory relevance *per se*.[10] Similarly, can we subsume Grantham's practical interconnections or Leonelli's data integration under the present approach? My response is that we can: conceptual, practical, and other kinds of integration can be understood as part of an explanatory endeavor, as long as the notion of explanation is conceived broadly enough. In order to do this, however, we ought to depart from unidimensional, monolithic approaches to explanation—such as exclusively mechanistic, reductive, or causal models—and adopt a more liberal stance. In making this suggestion, I am not downplaying the significance of refining mechanisms, individuating causal relations, and achieving local reductions, which constitute important explanatory practices. My point is rather that these are not the *only* significant kind of explanation in biology and, *a fortiori*, in science.

In sum, the present account differs from traditional interfield models by focusing on a single kind of interconnection and from mechanistic approaches by adopting a more liberal stance towards explanation. Still, despite these differences, the thesis defended here is best viewed not as a radical departure from previous work, but as an elaboration that replaces a gerrymandered set of interconnections with a single, more perspicuous one. At the same time, my liberal stance towards explanation invites a different kind of objection, namely that, without a specific working model of explanation the entire suggestion becomes vacuous. I will return to this trivialization worry in §6 below. Before doing so, I want to focus briefly on some advantages of the ER account.

In §3, I listed two independent desiderata for any general account of unification. First, any such account should motivate the significance of unification for scientific progress. Second, it must distinguish the various stages and degrees of the unification process. I now show that ER fulfills both conditions. Consider, first, the normative issue: why is unification important? Our discussion of evo-devo suggested that developmental studies indicate constraints on possible evolutionary trajectories of populations. Similarly, an evolutionary perspective is required to explain interspecific and intraspecific similarities among ontogenetic mechanisms. Succinctly put, without a synthetic framework encompassing both developmental and evolutionary resources, these issues cannot be meaningfully posed, let alone addressed. These considerations provide a general

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[10] I am grateful to an anonymous reviewer for raising this objection in a cogent fashion.

answer to the normative question: unification is an important scientific goal because it enables researchers to formulate novel questions, broadening the range of explananda, and indicates how these puzzles can be solved, enriching the bag of explanantia. Insofar as science strives to explain, unification constitutes an important aim.

A couple of clarifications are now in order. First, since explanation plays a prominent role in several other accounts of unification, it would be wrong to maintain that interfield and mechanistic models *lack* the resources to explain the normative significance of unification. Once again, my goal here is not to offer a radically different alternative, but to draw attention to a specific aspect of extant models—explanatory relevance—that captures the normative significance of unification in science. Second, I should clarify the nature of unification and the sense in which it is a general aim of science. The present treatment of unification is just as 'local' as typical accounts of integration, in the sense that it does not presuppose a homogeneous, metaphysically or methodologically unified picture of science (Mitchell [2003]; Plutynski [2013]). Explanatory standards vary drastically across scientific domains, and it would be preposterous to adopt a single measure that can be used to assess explanations in, say, physics, chemistry, biology, and psychology. Consequently, alleged cases of unification should be investigated individually, on a case-by-case basis, rather than as a general trend (Wylie [1999]). At the same time, I want to resist the temptation of dispensing with the idea of unification altogether and replacing it with local integrations. Assessments of explanatory relevance may be wildly heterogeneous across sciences, or even across subfields of the same science. Still, there is something that underlies all local integrations, something that allows us to apply the same concepts—unifications, syntheses, integrations, etc.—across the board: this is the relation of explanatory relevance. Hence, the present model of unification falls somewhere in between the grand unification of the reductionist school and the piecemeal approach advocated in much contemporary philosophy of science. The ER condition allows us to treat unification as a general aim science, while eschewing the controversial assumptions of a metaphysical foundation, a shared methodology, or a single theoretical framework. In a sense, it combines the flexibility of integration with the generality of classic reductive unification.

Moving on to the second desideratum, what marks the stages of the unification process? To address this question, it is important to note that integration is best conceived not as an absolute 'all-or-nothing' matter but as coming in degrees. This was already recognized by Kincaid and Grantham, but the present account is different in three important respects. First, on the view defended here, the degree of integration does not depend on the kind of inter-theoretic *connections*, but on the number and relative weight of inter-theoretic *explanations*. Consequently, the synthesis of two fields begins as soon as a new question is posed that requires an integrative framework, and the degree of unification increases proportionally to the amount and significance of puzzles and explanations thereof. Given the difficulty of quantifying the degree of unification in absolute terms (fields A and B are unified to degree x), unification can be viewed from a *contrastive* perspective: A and B are more (or less) unified than they were before, or than other fields C and D. However, unification has no pinnacle or 'upper bound.' Since, in principle, there is no limit to the number of questions that can be addressed, one never reaches a stage of maximal unification; connections between field can always be furthered by posing new problems and offering novel solutions. Borrowing an expression from Kitcher ([1999]), full-blown unification is best seen as a 'regulative ideal,' as opposed to a general characterization for the current state of science. While one can meaningfully determine whether two fields are in the process of being unified or of increasing their degree of synthesis, asking whether they are unified *tout court* is an ill-posed question, as complete integration occurs only in the limit.

A second difference is that, while previous accounts of unification are necessarily symmetric, the ER condition can be weakened to allow for asymmetric unifications. To illustrate, insofar as unity is measured in terms of interfield connections, it is impossible for field A to be connected to field B, but not vice versa. Likewise, the modeling of an inter-level sophisticated mechanism presupposes the contribution of both *integranda*. In contrast, if unity is conceived as explanatory relevance, it is possible for A to be relevant to explanations in B, while B-concepts and B-methods cannot be (presently) employed in A. While the above formulation of ER fits a stronger form of symmetric unification, characteristic of paradigmatic cases of inter-level and mechanistic unification, a weaker asymmetric formulation of ER (which drops the 'vice versa' clause) covers instances of genuine reductions and explanatory extensions.

Third, ER renders unification a temporal and reversible stage, which can be effectively lost and achieved again at a later stage. This feature nicely captures various episodes in the history of science, such as the relation between embryology and evolution which, as noted above, were connected during the 19th century, became effectively separated during the foundation and development of the modern synthesis, only to be reunified once again with the advent of molecular biology. These 'transient' historical relations—which are featured in some accounts of integrations (Brigandt [2010]; Plutynski [2013])—are hard to reconcile with traditional accounts of unification. Both reductive and non-reductive models implicitly assume that unification is independent of the current state of a field: once two fields are synthesized, they can only be separated if the derivative reduction is shown to fail, or if the interfield theory was flawed; but, in such cases, we ought to concede that the two disciplines were never really unified in the first place. A similar dilemma also affects mechanistic accounts: a loss of unification requires the inadequacy of interlevel mechanisms which, in turn, presupposes that the alleged unification was either mistaken or unnecessary. In contrast, the cross-temporal dimension of unification makes perfect sense on the ER model. Ontogeny and phylogeny were unified after Darwin because both frameworks were required to address certain questions, despite the lack of adequate causal-mechanistic explanations. Subsequent progress in the field of genetics necessitated a disciplinary disconnection—and, thereby, a loss of synthesis—in order to black-box developmental mechanisms, which became explanatorily relevant to evolution, once again, with the emergence of new puzzles and solutions. In short, ER allows for the loss or weakening of unification for the sake of the advancement of science, only to be regained at a later stage.

6 Concluding Remarks

Over three decades ago, Maull and Darden noted that integration is motivated, at least in part, by the emergence of questions that cannot be addressed with available concepts and techniques and, when this happens, it becomes necessary to broaden the scope of the original fields by establishing interconnections. Elaborating this insight, I advanced a notion of *explanatory relevance* that preserves the notion of scientific progress underlying the reductive enterprise while eschewing (at least some) problems. Unification is a variety of explanatory extension that not only uncovers the schematic premises of problem-solving patterns—the theory's 'axioms'—but also poses and addresses new problems.

I now conclude the discussion by addressing two significant worries. First, some critics might argue that the present account makes unification too 'cheap.' If explanatory relevance is all there is to unification then, in order to initiate the synthesis of two fields, it is sufficient to formulate a question that requires the integration of both disciplines. However, the objection runs, this is subject to trivialization. Consider the following hypothesis: neutrinos are faster than the speed of light and, based on a trophic-dynamic analysis, coral reefs are well-formed ecosystems. Conjunctive statements of this kind require the conceptual apparatus of both particle physics and ecosystem ecology; they cannot be addressed by either individually. Yet, it seems preposterous to conclude that these disciplines are in the process or in need of integration on the basis of such gerrymandered hypotheses. Hence, unless we provide a more specific notion of explanatory extension, ER is too liberal a condition for unification.

This trivialization worry is a substantial one, which ought to be addressed with the utmost care. One solution would be to dismiss *ad hoc* hypotheses on the basis of their logical form, for instance, by ruling out conjunctive or disjunctive statements by *fiat*. This strategy, however, is hopeless, because identical problems arise with conditionals ('if neutrinos are faster than light, then coral reefs are ecosystems') and other statements that cannot be so readily discarded. A more promising alternative is to appeal to the in-principle-separability of the two conjuncts, which can be addressed independently without moving across levels or fields. The problem here is that concepts such as separability cannot be simply assumed, but require careful analysis, and the notorious difficulties that undermined logical empiricism should make us wary of any attempt to isolate classes of genuine scientific hypotheses in general or formal terms. This brings us back to the original question: do conjunctive statements like the one above initiate the unification of physics and ecology?

Let us step back and address the issue from a slightly different perspective. Philosophical discussions have often overlooked that unification does not *always* further the advancement of science. In addition to remarkable results, such as the physicochemical theory of the molecular bond or the modern synthesis of genetics and evolution, there are instances of unifications that have not achieved the same degree of success—early attempts to bring together electronics and neuroscience have not been very effective—or, worse, synthesis can also trigger mediocrity when it encourages researchers to straddle multiple fields without having real expertise in any one. What distinguishes useful unifications from useless ones? While other accounts remain moot on this point, ER provides at least a sketch of an answer: insightful questions lead to 'progressive' unifications whereas trivial or misleading questions trigger 'regressive' ones. Applying this insight to the above trivialization worry, it follows that *ad hoc* questions do underlie potential integrations, albeit degenerate ones that play no role in science. In other words, one could in principle advocate the unification of physics and ecology on the basis of gerrymandered hypotheses like the one above. The appropriate response is not to reject it *qua* unification but, rather, to dismiss it as a *useless* unification. Some readers will complain that I have just swept the dirt under the rug, for now the problem becomes distinguishing between 'progressive' and 'regressive' unifications or explanatory extensions, which presupposes a general account of the pragmatics or relevance of explanation—a daunting task that cannot even begin to be adequately addressed here. Does this mean that we are back to where we started? I believe that it does not. What this shows is that appealing to explanatory relevance, by itself, does not *solve* the issue of scientific unification but, rather, *subsumes* it under a broader, independent task: the problem of specifying a general criterion for evaluating explanations. While there is undoubtedly more work to be done, reducing a more specific problem to a more general one constitutes a significant advancement.

Other readers might raise a different objection, namely, that ER is irrelevant for assessing the debate over the unity of science. The notion of explanatory relevance has epistemic significance but bears no metaphysical import and, consequently, explicitly removes the issue of the methodological unity of science from the question of its metaphysical foundations. To wit, debates over the ongoing evo-devo synthesis are completely independent of whether one sides with the fundamentally cohesive view of science of Carnap, Oppenheim, and Putman, or with the fragmented picture of the Stanford School. This, however, raises a worry that the crucial issue is being avoided, a critique that has been raised against interfield theory (Dupré [1993]) and could also be directed against the present model. This second objection suggests a conceptual shift. To avoid getting entangled in a futile dispute on the 'true meaning of unity,' it might be better to start afresh. Perhaps we should set the hackneyed term 'unity' aside and rephrase the debate in terms of some alternative notion. A plausible candidate would be *interdisciplinarity*, a closely connected concept that is widely employed both in technical and popular literature, but is seldom articulated an precisely defined.[11] Alternatively, one could could also replace 'unity' with

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[11] It is common to define an area of study as 'interdisciplinary' when it transcends traditional disciplinary boundaries. Yet, a truly interdisciplinary field of research does not merely span two or more fields; it must also advance conceptual and experimental knowledge, shedding light on problems that previously seemed intractable and posing new questions that cannot be raised and addressed in the original frameworks. To be sure, 'unity' and 'interdis-

synthesis or *integration*, as long as the local nature of these processes does not thwart the general contribution as a 'regulative ideal' in science. Still, terminological choices should not be overemphasized: whether we ultimately refer to the enterprise as 'unity,' 'interdisciplinarity,' 'synthesis,' 'integration,' or as something else, the important point is that the notion of explanatory relevance is what motivates and grounds the integration of scientific fields.

In conclusion, our discussion has focused on the biological sciences. The extent to which it can be applied to other natural and social sciences is an important question that, however, must be set aside for a different occasion. For the time being, the 'unity of science,' understood in terms of ER, is best viewed as a working hypothesis. Yet, contrary to the working hypothesis advanced by Oppenheim and Putnam over half a century ago, the regulative ideal of unificatory explanation seems to conform quite well to actual scientific practice.

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ciplinarity' are hardly synonymous. Interdisciplinarity often carries a connotation that the involved disciplines are importantly distinct and thus arguably disunified. In addition, appeals to interdisciplinarity often presuppose specific references to social aspects of science, such as funding and institutionalization. Still, a shift from talk about unity to talk about interdisciplinarity—or some related concept—along the lies of suggested by ER would be welcome in many respects. In addition to setting aside metaphysical worries about foundations, it would mitigate trivialization worries: whereas the notion of 'regressive unification' might strike some readers as puzzling, 'regressive interdisciplinary domains' are commonplace in many areas of research.

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