Do we need a ‘theory’ of development?

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Abstract

Edited by Alessandro Minelli and Thomas Pradeu, *Towards a Theory of Development* gathers essays by biologists and philosophers, which display a diversity of theoretical perspectives. The discussions not only cover the state of art, but broaden our vision of what development includes and provide pointers for future research. Interestingly, all contributors agree that explanations should not just be gene-centered, and virtually none use design and other engineering metaphors to articulate principles of cellular and organismal organization. I comment in particular on the issue of how to construe the notion of a ‘theory’ and whether developmental biology has or should aspire to have theories, which four of the contributions discuss in detail while taking opposing positions. Beyond construing a theory in terms of its empirical content (established knowledge about biological phenomena), my aim is to shift the focus toward the role that theories have for guiding future scientific theorizing and practice. Such a conception of ‘theory’ is particularly important in the context of development, because arriving at a theoretical framework providing guidance for the discipline of developmental biology as a whole is more plausible than a unified representation of development across all taxa.

Keywords: theory, explanation, development, genes, developmental biology

Developmental biology is a major area of contemporary biological research, and its historical forerunner embryology has been no less important. At the same time, engagement with developmental biology by philosophers has been relatively sparse. Apart from evolutionary biology and systematics, recent philosophy of biology has focussed on genetics and molecular biology, and addressed developmental biology only in the context of individual topics, e.g., the idea of genetic programs, or in the context of evo-devo and thus evolution (for exceptions see Robert 2004 and Love 2015). Given this, especially philosophers ought to take a look at the recently published collection *Towards a Theory of Development*. Co-edited by a biologist (Alessandro Minelli) and a philosopher (Thomas Pradeu), it combines valuable contributions by biologists and philosophers alike, prefaced with forewords by Brian Hall and by Richard Burian.

I begin with surveying the diverse theoretical perspectives included in the volume, which make it so interesting and clearly broaden our vision of what phenomena are part of development. After briefly taking a look at the role that the contributors accord to genes in explanations of development, I will discuss the 'theory of development' issue raised already in the collection's title (which echoes the title of a 1975 paper by Lewis Wolpert and J. H. Lewis). This is of particular significance, given that four of the contributions (by Wallace Arthur, Lucie Laplane, Alan Love, and Thomas Pradeu) explicitly address how to construe the notion of a 'theory' and take conflicting positions on whether there are or how important it would be to have theories in developmental biology. My commentary aims to shift the focus away from the empirical content contained in theories toward how theories guide future theorizing and practice. For while a theory of development offering a unified representation of development across diverse taxa is unlikely to be had, establishing a theoretical framework that offers guidance for all of developmental biology would be desirable.

Diverse aspects of and perspectives on development

Even though the development of plants is unfortunately discussed in only one contribution (by Michel Vervoort), some of the chapters indeed aim to capture phenomena that have not usually been addressed as part of development, so as to widen the boundaries of development and broaden our vision of what development is (see also Pradeu et al. 2011). In what is my favourite essay of the volume, Alessandro Minelli (2014) takes on what he calls the adultocentric perspective, which assumes that development always begins with an egg and is finished with a reproductively capable adult, that development includes for the most part only the formation of adaptive traits, and that it is irreversible. Further common assumptions are that development exists only in multicellular organism and that, being about morphological traits only, development is distinct from metabolism. Minelli challenges every tenet of this stereotypical vision of development, based on a plethora of fascinating examples illustrating the diversity of life cycles. He points for example to the reversibility of cell differentiation in plants and microbial species, arguing that physiological changes in unicellular organisms ought to be included among developmental processes. Given the phenomenon of budding, Minelli's non-adultocentric, 'disparity view' of development rejects the notion that development begins with a fertilized egg. And by treating gametogenesis as a developmental process, many life cycles (even in animals) become multigenerational, where one of the generation is unicellular, providing an additional reason for including unicellular forms in development. The contribution by Spencer Nyholm and Margaret McFall-Ngai (2014) focuses on microorganism by addressing their causal contribution to the development of animals, including the formation of the gut and immune system, the induction of epithelial proliferation in gnotobiotic fish, and the morphogenesis of the Hawaiian bobtail squid's light organ. Other recent evidence for the profound impact of microorganisms pertains to the development of the central nervous system and includes long-term effects on behaviour.

Towards a Theory of Development also contains many different theoretical perspectives. Stuart Newman (2014) discusses factors only occasionally appealed to in explanations of development—the relevance of physical properties of cells and tissues, stemming from them being both soft matter and excitable media, i.e., being able to generate a response disproportionate to the physical stimulus. Probabilistic aspects of development are addressed by Jean-Jacques Kupiec (2014), who defends his position that gene expression is a stochastic process that is not just noise but essential for development by creating a diversity of cell types, where the underlying gene action is selectively constrained by cells and tissues. Introduced by Waddington, the historically prominent notion of an epigenetic landscape is still used by some contemporary theoretical approaches to development, in particular in the context of stem cells (Fagan 2013). Accordingly, the chapter by Giuseppe Fusco, Roberto Carrer, and Emanuele Serrelli (2014) discusses contemporary uses of the landscape metaphor, which among other things reveal how Waddington neglected stable, yet transitory cell types. Their verdict is that even if a landscape approach was able to account for cell differentiation, this does not include cell proliferation, movement, and death, the influence of extracellular material, and other aspects of pattern formation. As another theoretical notion with a significant past, Davide Vecchi and Isaac Hernández (2014) turn their attention to morphogenetic fields, combining a historical discussion of this idea with some recent perspectives. In addition to issues about causal responsibility, such as a specific cause vs. distributed, non-localizable causation (e.g., the instability of interaction dynamics), they wonder "what kind of things are fields? Are they entities or processes? Causes or effects?" (92). To my mind, this suggests that while it is tempting to endorse a process ontology for developmental and other biological phenomena, many ontological issues about processes yet have to be clarified—another domain where philosophers and biologists can fruitfully collaborate.

Given recent discussions of mechanisms, especially philosophers will want to take a look at the contribution by Johannes Jaeger and James Sharpe (2014). Considering dynamical models of gene regulatory networks underlying developmental pattern formation, they tackle the issue of how to individuate kinds of mechanisms. The motivation is that the same developmental outcome (e.g., a stripe pattern of a morphogen) can be produced by two or more causal networks that differ in some of the connections among genes, yet often such minor network variants should not qualify as separate mechanisms. To arrive at an account of what two genuinely different mechanisms are, instead of merely considering mechanism diagrams depicting network structure, Jaeger and Sharp advocate the mathematical analysis of dynamical models, which entails how two dynamical system's phase spaces differ regarding the number and locations of attractor points and other features. Scott Gilbert and Jonathan Bard (2014), in contrast, are more sceptical about the possibilities for using such models involving differential equations, on the grounds that most interaction parameters determining dynamical behaviour are not empirically known in living systems. Instead, they see the systematization and formalization of knowledge about development to come from graphs capturing different entities and the kind of relations among them (e.g., activates, or migrates)—an approach similar to formal ontologies in information systems.

Yet another intriguing perspective is how James Griesemer (2014) elaborates on his previous account that development is the acquisition of the capacity to reproduce, by adding the notion of scaffolding. Scaffolding has gained recent prominence as a mechanistic account of inheritance in various domains, including cultural inheritance (Caporael et al. 2014). In the present context, the scaffolds are molecular, cellular, or histological structures, e.g., the mesoderm functioning as a scaffold for the formation of the vertebrate neural plate. Given that a scaffold is typically outside of the system using it, scaffolding essentially includes a system's environment, although in Griesemer's case all of this takes place within organisms, so that his approach "pushes the 'eco-devo' perspective inside the body of the fly" (193). Griesemer reasserts his prior tenet that any kind of reproduction involves material overlap, but does not consider that scaffolding also provides a means of inheritance without material overlap (Sterner forthcoming), which would have additionally enhanced the relevance of the ecological context advocated by him. Addressing viruses and the very origin of cells involving scaffolding, Griesemer notes that unlike the other contributors he does not assume that development is a *cellular* process.

Several of the contributors view considerations about evolution as relevant to theorizing about development. Newman clearly acknowledges that the physical interactions he focuses on had a primary causal role in development only in the earlier stages of evolution, while with the advent of multicellular organisms genetic factors have acquired more prominence. Thus, phylogenetic time matters for the nature of development, where Newman cautions against a uniformitarian view (as found in the Modern Synthesis) that assumes that a type of cause has the same relevance throughout evolution (see also Love and Lugar 2013). In his historical review of the rise of the notion of gene regulatory networks (GRNs), Michel Morange (2014) addresses how some developmental geneticists were tacitly or—as in the case of Eric Davidson—openly at odds with the Modern Synthesis, again on non-uniformitarian grounds, though in this context the objection is to treating all genes' evolution on par, given that overall GRNs are hierarchically structured where some aspects of GRNs (corresponding to the origin of higher taxa) are upon their origin much harder to modify in evolution than other parts of GRNs. Morange also ponders the existing gap between the description of concrete GRNs and the abstract framework of evolutionary theory, suggesting that a theory of innovation may come to bridge it.

Armin Moczek (2014) advocates for "nesting a theory of development within a theory of developmental evolution" (218). He lays out a fruitful methodological framework for investigating the development of organismal traits from a phylogenetic perspective, by locating traits in a nested hierarchy of homologues and investigating the patterns and causes of their variation. The chapter by Michel Vervoort (2014) makes the bold proposal that a theory of development can be established by finding convergent developmental processes that are present in *all* organisms displaying development. He points to some such features found in animals and plants alike. While this focus on convergent features takes an evolutionary perspective, by excluding developmental processes shared due to common ancestry it is meant to arrive at principles of development that are "independent of the evolutionary position and history of the different organisms" (203). Yet to my mind, even convergence-creating conditions are not fully independent from historical contingencies (as Vervoort's agenda requires), and conversely, cross-taxa developmental features due to homology may well have a place within a theory of *development*, as only their evolutionary interpretation differs.

Beyond gene-centered approaches and engineering metaphors

A good deal of experimental investigation in developmental biology is gene-centered, in that manipulations of DNA sequences and the activity of genes, e.g., by means of knockout experiments, provide informative clues about the developmental role of genes. Yet from an experimental methodology that investigates the impact of individual genes one cannot infer that non-genetic factors are causally irrelevant (Robert 2004). Gene regulatory networks (GRNs) are clearly important for explanations of development (Davidson 2006), however, more than an appeal to genes is needed. The reason is that an explanation of development has to account for cell differentiation and tissue formation in different parts of an individual, and thus to include the differential expression of genes across space and developmental time. The transcription of a gene is regulated by transcription factors and other non-genetic entities; and upon the formation of an RNA transcript, the final product is often due to alternative splicing and other post-transcriptional processes, which are again regulated by non-genetic entities (Griffiths and Stotz 2013). In addition to how within one cell the diversity of products created from a single gene is regulated across time, differentiation across an organism's cells is modulated by the interactions among cells. The idea that gene activity's crucial importance to cell differentiation does not entail a priority of genes is also echoed in Wallace Arthur's (2014) chapter, who asserts that cell differentiation is instead "the result of *an interplay* between genes and other molecules, an interplay that is in many cases also influenced by environmental factors" (147).

How do the other contributions in *Towards a Theory of Development* stand on the centrality of genes in explanations of development? Brian Hall's (2014) foreword summarizes it as follows:

> I can hear the murmurs through the ether: but surely any theory of development must be gene based? Not according to theories discussed herein, which include emphases on morphogenetic fields, cell differentiation, natural selection, disparity, plasticity, stem cells, dynamical systems theory, and more. (x)

To be sure, Michel Morange's chapter focuses on gene regulatory networks, however, his historical review of the rise of this approach (and its relation to evolutionary theory) does not amount to an endorsement of a primacy of genes. The mathematical models of Jaeger and Sharpe (2014) pertain to gene regulatory and signalling networks, but even they acknowledge that "there are other essential components of developmental systems" (58).

While viewing his epigenetic approach as something to be linked to genetic determinants of development, Stuart Newman unsurprisingly emphasizes physical properties of cells and tissues. Jean-Jacques Kupiec's (2014) stochastic account of gene expression entails that "development is not driven by gene networks but by this intrinsic probabilistic process. Thus, the genetic programming theory of development is no longer valid" (165). The development as the acquisition of the capacity to reproduce perspective endorsed by James Griesemer (2014) puts forward concepts of development and reproduction that are explicitly meant to "address limitations in treatments of units of heredity and evolution that presupposed evolved characteristics of genes" (190). As mentioned above, his scaffolding approach takes an eco-devo perspective within an organism, and he specifically views the genome as a scaffolding infrastructure used by the developmentally responsive transcriptome. In addition to viewing morphogenetic fields as something that should not be reduced to a purely geneticised concept of positional information, Vecchi and Hernández (2014) oppose the genetic reductionism of philosopher Alex Rosenberg (1997) by noting that "progress in developmental biology has been parasitic on increased knowledge concerning the mediators of molecular interactions, namely cells" (92). In a similar vein, Gilbert and Bard (2014) state that "a theory of development cannot be a subset of a theory of genetics because much of development is not run by the genome" (139). What should be especially interesting to philosophers is that they explicitly endorse the notion of *downward causation*, on the grounds that higher-level features place constraints on what lower-level interactions are viable.

While the accounts in the volume under discussion are anything but gene-centered, they should not be taken as fully representative of developmental biology. For at least regarding experimental methodologies, a good deal of developmental biology is centered on studying the impact of gene activities, even though signalling and other pathways involving non-genetic entities are in view, as well as entities on and above the cellular level. The present authors clearly take a broad and reflective perspective on what an adequate explanation of developmental phenomena has to cover, including among other things phenotypic plasticity and thus the impact of the environment. But I would like to note that it is non-trivial that a broad perspective would lead to a non-gene centered approach. For several of the contributors include evolutionary considerations apart from development as such, yet historically an evolutionary approach has been influential in promoting the notions of 'genetic information' and 'genetic program,' where natural selection is seen as creating and transforming such information (Maynard Smith 2000; Mayr 1994). And even in contemporary evo-devo, the idea that evolution is to be explained in terms of changes in gene regulatory networks is prominent (Davidson 2006; Erwin and Davidson 2009). But in any case the role of genes in evolution and in development must not be conflated (Brigandt 2013a, sect 5); and despite his evolutionary approach, in his chapter Armin Moczek (2014) is clear regarding explanations of development:

> … the metaphors of genes and genomes as blueprints of development, and the separability of genes and environment as contributors to trait formation, have outlived their usefulness … (223)

A related issue is attempting to understand developmental systems by using engineering notions. Apart from a stereotypical neo-Darwinian perspective that construes traits as evolved designs and views organisms as evolved machines (Dawkins 1976), contemporary systems biology often uses design and other engineering notions (Alon 2007; Braillard 2015). While this is occasionally motivated by adaptationist assumptions or the strategy to reverse engineer organismal systems (Csete and Doyle 2002), for the most part systems biologists search for 'design principles' that more generally describe organismal functioning across different contexts, so as to have theoretical principles beyond sheer data about molecular details (Poyatos 2012). Still, others have cautioned against the use of information, machine, and other design metaphors. One reason is that in various contexts they are empirically inadequate (Boudry and Pigliucci 2013). For example, phenotypic plasticity is a feature of many organisms that is clearly disanalogous to machines, and the same holds for robustness as a common property of molecular, cellular and organismal systems (Brigandt 2015; Kirschner et al. 2000). Jaeger and Sharpe (2014) note this in their chapter:

> The second way in which the computing metaphor appears problematic lies in … how [computer programmes] respond to changes. The vast majority of random changes to a human-engineered computer programme will cause it to malfunction, whereas the same is not true for mutations to biological systems. (65)

The flexibility of cells is also echoed by Vecchi and Hernández (2014), when they state that "there remains a world of difference between treating cells as programmed machines and treating cells as interpreting agents" (91). Apart from empirical inadequacy, an additional reason is that the use of information and machine metaphors is bad for science education and the communication of biology to the general public, as witnessed by the attempt of intelligent design proponents to use such metaphors to further their anti-evolutionary agenda in the public arena (Brigandt 2013b; Pigliucci and Boudry 2011).

Interestingly, the contributions in *Towards a Theory of Development* do not use design notions or engineering perspectives, with the exception of Jaeger and Sharpe's appeal to design principles from the perspective of systems biology.[1] Vervoort's (2014) approach to establishing a

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[1] The dynamical systems theory approach employed by Jaeger and Sharpe has also been used in an argument

theory of development by convergent developmental features across animals and plants is clearly after underlying principles and invokes natural selection, yet he does not use the notion of design at all.

The notion of a theory and the relevance of a theory of development

In their editors' introduction, Minelli and Pradeu (2014a) state that "The present volume addresses the question of what theories are, or could be, in developmental biology" (1).[2] Actually, several of the contributions do not comment at all on whether developmental biology has or should have theories—which in my view is a positive thing, in that several important theoretical perspectives on development can be put forward even if the authors do not agree on a particular definition of 'theory' or the relevance of theories. Some of the contributing biologists merely point to some features that would have to be included for it to be a *general* theory of development. For example, while acknowledging that it pertains more to the historical origination of morphologies, Newman views physical properties of tissues as a starting point for a developmental theory. Both Verwoort and Moczek indicate that a theory of development needs to hold for diverse taxa. The former, as mentioned, views such a theory as laying out convergent features shared at least by animals and plants, while for Moczek the theory needs to be "applicable to a wide range of organismal diversity and across levels of biological organization" (218-219). Although addressing the notion of a theory only in passing, these remarks imply that these biologists construe the idea as *one* overarching theory and at the same time assume that

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against the mechanistic and engineering approach common in some areas of systems biology to decompose a system and understand the functioning of modules in isolation from each other (Huang 2004).

[2] For discussions of what theories in overall biology are, see Pigliucci et al. (2013).

there is no such theory yet.

Wallace Arthur (2014) is the biologist offering the most direct reflection on the meaning and status of theories in developmental biology. He astutely notes that the volume title *'Towards a Theory of Development'* boldly implies that:

> first, that a single theory of development is at least possible; second, that we do not yet have one; third, that it is desirable to seek one; fourth, that we have a consensus on what is meant by 'a theory' in the biological sciences; … (144)

An interesting angle is his suggestion that something can be meaningfully called a theory only if one can state a possible rival theory, such as the Darwinian as opposed to the Lamarckian theory in evolution. Even though there were in fact opposing theories in the history of genetics and the history of embryology, e.g., preformationism vs epigenesis, Arthur insists that this does not hold for modern developmental biology, where textbooks are not structured by major debates among alternative theories. Given that we do not know about any rules that would specify the relative importance of different abstract causal networks in complex developmental systems, his verdict is that "as of now we do not have a single theory of development" (150)—a view also found in the contribution by Gilbert and Bard (see also Minelli 2011).

Three of the contributions by philosophers discuss the theory question in detail. While Thomas Pradeu and Lucie Laplane articulate a notion of 'theory' and maintain that there are in fact theories in developmental biology, Alan Love (2014) takes the opposite approach by in a sense even arguing that no theories of development are needed. Based on bibliometric evidence, Love starts with the observation that the t-word is rarely used in developmental biology. He rejects two possible interpretations of this situation: that there are theories which (even though developmental biologists do not call them such) one can reconstruct from the knowledge of the field, or that contemporary developmental biology is a relatively immature field and yet has to generate theories. Instead, Love wants to take the scarcity of references to theories at face value, and argues that developmental biology gains stability and structure not from the presence of theories, but from scientific questions. This he dubs the erotetic organization of developmental biology ('erotetic' = pertaining to questioning). On this view, there are domains of problems ('problem agendas'), which are investigated across longer periods of time and provide structure to knowledge (see also Love 2013). Love illustrates this by comparing different editions of developmental biology textbooks. While of course the particular content has changed during the last two decades, a textbook's chapter organization remains stable, structured in terms of issues and kinds of phenomena, e.g., 'patterning the vertebrate body plan' or 'cell differentiation.'

Pradeu (2014) rightly objects that "science needs not only problems; it needs *answers* as well" (23)—answers which may be theories—but Love's distinction between theory-informed science and theory-directed science shows that his position is more subtle. Love actually acknowledges that developmental biology uses theoretical knowledge and is informed by different theories, but his point is that in developmental biology such theories do not direct investigation and structure knowledge. What I view as the great virtue of his account is that also those insisting on the centrality of theories for developmental biology can take on board the insight that stable questions are one factor providing theoretical structure and intellectual identity to certain areas of developmental biology.

Pradeu directly challenges the consensus position that there are no theories in developmental biology. As an initial reason to be suspicious of the consensus, he points out that other biological fields offer theories and that in its history even developmental biology (i.e., embryology) put forward theories—an argument not cogent in light of Arthur's point that an actual comparison of past and present developmental biology shows significant differences in terms of references to theories. Looking at standard criteria for being a theory, such as high generality, high level of abstraction, or the use of mathematical models, Pradeu rejects them on the grounds that the clonal selection theory meets none of them. To my mind, this is to discard a potentially important notion of a theory simply based on one counterexample that implicitly relies on a different use of 'theory'.[3] Here is Pradeu's preferred notion, which is to yield that developmental biology has theories:

> As a reasonably demanding definition of a scientific theory, it is possible to suggest that a theory is a structured set of testable explanatory and predictive hypotheses. (22)

The dialectic of the overall discussion is somewhat ambiguous, given that he proceeds as follows: "So, what exactly are the roles that are played by scientific theories and cannot be played by something else? … First, theories make possible *explanations* and *predictions* … A second role of scientific theories is *unification*." (23-24). The first aspect of explanation and prediction is unassailable—although it trivially follows from Pradeu's prior definition (as opposed to first picking out some features that have been associated with theories, showing why this yields a philosophically interesting notion, and finally codifying this as one's definition). The second aspect about unification, however, is not always true if one uses his definition, according to which *any* body of explanatory and predictive claims is a theory. One could have included unification explicitly in the definition, but my impression is that Pradeu would not want too restrictive a notion of a theory, given his position on the prevalence of theories in

[3] In fact, one reason for why the term 'theory' is rarely used in developmental biology as compared to evolutionary biology and ecology (as evidenced by the bibliometric data with which Pradeu starts out, but which he does not analyze) is that scientists often identify theories with mathematical frameworks.

developmental biology.[4]

The account of Laplane (2014) is more transparent. She starts with Darwin's defense of his evolutionary theory, which reveals

> the criteria that we think useful for the identification of theories—namely the explanation of 'independent classes of facts'. (249)

Closely related to the traditional idea that a theory offers unification, this is indeed a philosophically significant notion of a theory, which Laplane then uses in her insightful discussion of the cancer stem cell theory. The latter is the scientific idea that some, but only a small proportion of the cells in a cancer tissue have stem cell-like properties (i.e., the ability to self-renew and generate different types of cancer cells). A major line of evidence favouring this idea over the classical view is its ability to explain several independent facts, which otherwise have to be explained separately, using different additional assumptions.[5] While scientists sometimes call it a 'model' or a 'hypothesis,' Laplane has offered a principled reason for why it is in fact a theory. In his chapter Pradeu also mentions several examples of contemporary developmental biologists actually using the term 'theory,' e.g., a theory of positional information and a cell fate theory (21-22). However, given that this is merely among his initial reasons for being sceptical developmental biology not having theories, Pradeu does not go into an analysis of the epistemic characteristics and significance of the theories he mentions (as Laplane does for

[4] Moreover, including unification in the definition of 'theory' would render false Pradeu's claim that making explanation and predictions "cannot be played by something else" but theories.

[5] The cancer stem cell theory can explain the facts that cancer cells often have a low ability to divide and create an entire clonal population, that non-metastatic cancer cells are present at distance from the primary tumor, that relapses after apparently successful cancer therapy occur, and that cancer cell populations are heterogeneous. Accounting for the latter without the cancer stem cell theory would require invoking mutation and selection within cancer tissues.

the cancer stem cell theory), nor does he address whether the same notion is behind all these uses of 'theory' in developmental biology.

While, as mentioned, some biologists may in line with the vision expressed in the volume's title ('Towards a Theory of Development') have one overarching theory in mind that is yet to be established, note that this is not offered by Pradeu's or Laplane's account that there already are several theories in developmental biology. Although Laplane maintains that "The CSC [cancer stem cell] theory is a theory *of* developmental biology" (255, emphasis added), she actually points to one theory within developmental biology, pertaining to one area of it. While Pradeu takes himself to have refuted the position that "developmental biology … is not structured by theories" (15), he at most shows that different parts of developmental biology are structured by different theories.

My general opinion is that there is more than one legitimate notion of a theory. And rather than offering a definition that holds for any scientific domain (e.g., in terms of prediction, explanation, or unification), we gain more traction by using a notion of 'theory' geared towards a particular empirical context. In many scientific areas, a theory has to be quantitative, though this will only be a desideratum in certain contexts in developmental biology. Any theory should have some contextually defined generality, which for the purposes of developmental biology means that such a theory at the least go beyond the welter of biological data by exhibiting principles of organisms' organization and of the organization's transformation in ontogeny. It is legitimate to require more, for instance, that any developmental theory hold for a larger group of taxa. But being able to capture both animal and plant development in one theory is implausible.[6] Thus, as

[6] While Vervoort's contribution tries to argue that there are informative cross-kingdom commonalities, he is clearly aware of the possibility that most commonalities may be more platitudes than principles. This is exacerbated

opposed to offering a general definition of 'theory' and trying to argue that there are theories (or that are no theories) in developmental biology, what I view as the more relevant philosophical project is to analyze the epistemic features of a particular developmental model (regardless of whether it is called a 'theory') or to discuss the empirical features that a framework yet to be established would need to have.

Here is another suggestion of mine for approaching the notion of a theory, which I take to be more important. Typically a theory is seen in terms of its *empirical content*, such as the predictions of biological phenomena and explanations of biological facts on which the definitions of Pradeu and Laplane focus. On any such approach the question is what kind of empirical content is needed to qualify as a theory, e.g., not only describing but causally explaining, or unifying disparate phenomena (such as animal and plant development). But in addition to content representing natural phenomena, there are also ideas *guiding scientific practice*, both experimental investigation and theorizing. And a theory may also do the latter. For instance, apart from embodying various explanations, evolutionary theory directs theorizing in many biological fields—not only putting a constraint on the establishment of knowledge (that it be consistent with evolution), but providing ideas and opportunities for the generation of knowledge in different fields. When discussing theories, including in the context of developmental biology, recognizing guidance for scientific practice in addition to content representing natural phenomena is important. For while the latter pertains to the status quo—the explanations and predictions that can be derived from a theory's content are already contained in the theory—guidance pertains to future theorizing and experimental practice and thus is forward-looking.

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by the fact that no other contribution in the volume discusses plant development.

This shift advocated by me toward how theoretical ideas guide future practice is foreshadowed by some of the volume’s contributions. Love calls for “analysing the use of theories to *achieve specific epistemic goals*. If we try to understand what theories are through the lens of what theories *do*, the structure of scientific theories is cast in a new light” (37, emphasis added). Griesemer (2014) explicitly distinguishes different aspects of a theory: “scientific theories [should] be conceptualized as comprising three kinds of components: a set of core principles, at least one family of models, and a theoretical perspective” (183). Griesemer’s discussion focuses on core principles (the principle articulated by him that development is the acquisition of the capacity to reproduce) and thus empirical content, without discussing theoretical perspectives in the concrete context of development. But in general terms he states that “a theory also needs a ‘theoretical perspective’ that can coordinate empirical investigative strategies … Theories, through their theoretical perspectives, function to guide empirical research” (200). Moczek (2014) mentions a traditional definition of theory in terms of empirical content,[7] but his overall discussion lays out a theoretical *methodology* for developmental biology (rather than the content of a theory of development). He proposes a fruitful two-step procedure, in which upon the accumulation of a data base theoretical knowledge is constructed using a three-level approach covering homology, developmental descent, and the causes of developmental variation. Applying this to the case of insect appendage development, an advantage of his theoretical methodology is that it does not require a particular starting point or directionality, as researchers can begin with any kind of trait on any taxonomic level.

Love’s problem agendas also provide guidance for practice and theorizing, including the

[7] “I would consider a theory of development any conceptual framework that is applicable to a wide range of organismal diversity and across levels of biological organization and which would allow us to identify, understand, analyse, and derive predictions about the nature of development.” (218-219)

coordination of ideas across different biological fields. This process of integrating knowledge is due to problem agendas having associated standards of how an adequate framework would look like (Love 2013; see also Brigandt and Love 2012). While Love wants to study theories in terms of what they do within science (which could include providing guidance for cross-disciplinary research), he still maintains that in developmental biology it is not *theories* that structure knowledge, but questions and problems.[8] In my view, it does not have to be either theories or questions—both may have some relevance for giving structure and guidance to theorizing in some parts of developmental biology. To be sure, representations of natural phenomena (i.e., theories as traditionally construed) are very different from scientists' values, such as the aim of answering questions and solving explanatory problems, so that including the latter among the features of a 'theory' may muddy the issue. However, my point is precisely that we need to move away from the philosophical focus on the empirical content of theories, and direct our attention toward theoretical knowledge more broadly construed, also including scientific aims, methodological and explanatory standards, and modeling strategies. For it is these latter features that guide scientific theorizing and practice (Brigandt 2013a).

Especially in the context of developmental biology does a discussion of the role of theories in guiding practice have distinct benefits. For comparison, consider Laplane's as well as Pradeu's advocacy of unification, which they construe as a state already achieved by a theory. One may well consider something a theory only if its content is unified, but this is a static vision of knowledge that falls short of a forward-looking perspective that includes methodological impacts on ongoing theorizing and a discipline's future status. A unified theory of development

[8] This opposition between theories and questions/problems suggests that Love likewise uses the traditional conception of theories in terms of empirical content only, so as to view other features of scientific theorizing and practice as outside of theories.

that captures animals and plants may well be impossible. Yet more plausible is a future theory that *methodologically* suggests how novel integrative knowledge about development can be generated. Given that a good deal of research in developmental biology still focuses on single model species, it would be a real achievement to have a developmental theory that provides intellectual strategies for developing knowledge pertaining to different taxa and levels of organization. Apart from upholding the mere aim of putting forward integrative explanations, this could involve exemplars and more abstract frameworks of how diverse items of knowledge can be coordinated, which can be fruitfully used regardless of whether one researches animals or plants. While in terms of empirical content, theories may only have a local validity, each pertaining to one part of developmental biology and representing only some of organismal diversity and complexity, there may be a theory of sorts that provides several crucial theoretical methodologies guiding and possibly organizing developmental biology as a whole.

Conclusion

Towards a Theory of Development is a highly recommended reading for everyone interested in developmental biology. By addressing various aspects of development—some of which have only recently come to be researched—and by providing many different theoretical perspectives, the volume not only lays out the state of the art in developmental biology, but also provides pointers for future investigations. Many contributions do not discuss the question of whether developmental biology has theories, but in my view it is actually more fruitful to present important theoretical frameworks than to ponder whether the notion of 'theory' applies. Given the complexity of organisms and the developmental variation across taxa, as well as the diversity of theoretical approaches in developmental biology, it is unlikely that there will ever be *a* theory of development—as opposed to several theories, each of which represents a local domain only. At the same time, I have tried to shift the focus away from the empirical content of theories (representations of organismal phenomena) towards ideas impacting theoretical methodology, such as explanatory and other theoretical aims, standards of explanatory adequacy, and modeling and other intellectual strategies. For by guiding theorizing and practice these features are forward-looking. While a unified representation of the development of animals and plants is implausible, it is more likely—and would be highly desirable—that a theory emerges that has an organizing influence on the *discipline* of developmental biology as a whole, by this theory providing some of the methodological guidance a developmental biologist uses, in particular theoretical strategies for using ideas beyond a single model species or level of organization.

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