

6

Integrating Composition and Process in Levels of Developmental Evolution

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Overview

Hierarchical organization in biology is usually conceptualized in terms of compositional levels of structurally defined entities. However, composition in biological systems is inescapably a dynamic affair concerning what a component *does* and not only what it *is*. This chapter examines how the dissociability of structure and function in complex evolved systems leads to ambiguities in the placement of things at levels, which makes “levels” a less useful concept. To address this difficulty, I develop a framework in which general levels of organization are restricted to levels decomposed under a specific causal process. In this approach, levels include only components and processes contributing to a focal process. After defining inter-level and intralevel relations in the process-relative framework, I explore a proposed decomposition of the process of developmental evolution. The resulting levels of developmental evolution are contrasted with levels of selection and replicator–interactor hierarchies.

6.1 Introduction

This chapter develops an approach to compositional levels in which composition is viewed as being relative to causal processes. I motivate this approach by first considering the roles that levels of organization play in biological theorizing as well as the difficulties of satisfying these roles. A major source of difficulties is that the same kind of component can have structural features that place it at one level and functional features that place it at a different level. Structural, functional, and hybrid structural–functional perspectives on levels each have limited resources to deal with this sort of problem. As an alternative, I explore a new approach based on functions understood as activities or processes, which contrasts with the standard understanding of functions as effects or outcomes. In the proposed approach, systems are “decomposed under a process,” so that a given hierarchy only includes the entities and activities that contribute to the same causal process. The central conceptual strategy for excluding causally irrelevant structure and function is to rely on a notion of constitution between processes to define placement into levels.

I then explore a proposed decomposition of the process of developmental evolution, the focus of evolutionary developmental biology. The levels of developmental evolution

exhibit the special property of “variational independence,” which grounds substantive insights about causation and generalization across levels, in line with the main roles for levels distinguished in the beginning. I close by showing how the processual framework improves on the effect-functional frameworks of levels of selection and replicator–interactor levels and sketch some directions for future work.

6.2 Theoretical Roles of Levels of Organization

The concept of levels of organization has many important roles in the life sciences. The investigation of how these roles should be fulfilled issues in corresponding tasks or problem areas for an account of levels of organization. Among these roles we can distinguish three that have broad significance:

(R1) *Composition*. To identify and describe general types of entities in terms of the types of parts they have as well as the types of wholes they compose.

(R2) *Causal segregation*. To demarcate types of entities that are such that (1) causal interaction occurs exclusively or primarily within types rather than between types, and/or (2) variables measured on those entities are causally independent of variables measured on other entities.

(R3) *Generalization*. To identify types of entities that cluster together in their scalar or qualitative properties such that these types support projection or inductive generalization.

In standard framings, levels of organization are populated by objects, individuals, or substances, but we can also ask about how other categories of items such as properties and processes are hierarchically ordered. (R1) can accordingly be expanded to be categorically inclusive: how should we characterize constitution or “making-up” relations between types of items across the wide variety of biological systems (see Gillett 2013a, this volume)? Some connections between categories will be explored in section 6.4.

(R2) refers to an idea that routinely arises in discussions of levels—that causal interaction occurs within a level or not between levels (Craver & Bechtel, 2007; Eldredge & Salthe, 1984; Wimsatt, 1976, 2007; see also Gillett, this volume). A similar idea is that levels track relations of conditional independence between variables, so that causal models of variables at one level of organization can safely ignore or background variables at other levels (see Woodward, this volume; Batterman, this volume). Different empirical and conceptual factors have been invoked to explain this “causal segregation” across levels of organization. One is that parts and wholes cannot stand in causal relations because they are not suitably distinct and causation is irreflexive (e.g., Craver & Bechtel 2007; Gillett, this volume; see Introduction, this volume). Another is that causal interactions are more frequent and stronger between items of similar space, time, and force scales (DiFrisco, 2017; Salthe, 1985; Wimsatt, 2007). Finally, evolution under selection may lead to modular body plans in which interaction across modules is limited (Simon, 1962). Nonetheless, the life sciences are full of examples of causal interaction crossing levels, and so causal segregation is more plausibly interpreted as a general pattern rather than a law (DiFrisco, 2017). This has the consequence that causal segregation, even if it is an important feature of levels, will not be useful as a criterion for assigning items to levels.

The combination of (R1) and (R2) puts multiple ontological categories at play. Even if levels of organization are primarily serially ordered collections of *objects*, these collections are supposed to ground certain kinds of interactions, causal processes, activities, or dynamics. In turn, regularities deriving from general typologies of composition (R1) and causation (R2) support inductive generalizations about levels (R3).

The most in-depth discussion of (R3) can be found in Wimsatt's work (1976, 2007), where levels are pictured as "meshes" of different sizes that converge on groups of entities that are clustered together in spatial scale and other properties. These levels can be regarded as loci in type space where densest similarities in structural and causal properties are to be found. Otherwise expressed, levels are "local maxima of regularity and predictability" in the space of different modes of organization of matter (Wimsatt, 1976, 237–238; 2007, 209; this volume).

In general, the more roles or purposes there are for the same concept, the less likely it is that one and the same version of that concept will be able to fill all of the roles. Prioritizing (R2) may promote criteria for distinguishing levels other than compositional criteria (R1), such as space, time, or force scale (DiFrisco, 2017; O'Neill et al., 1986; Rueger & McGivern, 2010; see Batterman, this volume). These "causal" levels are then unlikely to track composition relationships between types very closely. Similarly, pursuit of (R3) may pull in a different direction than (R2) and especially (R1). This would occur when the "maxima of regularity and predictability" at different scales pick out entities that do not stand in neat causal and compositional relationships with one another. Some examples of this divergence between (R3) and (R1) in the context of developmental evolution are examined in section 6.5.

Whenever a single concept is enlisted for many heterogeneous investigative roles, an attractive strategy is to give a pluralistic reinterpretation of the concept. Implementing this strategy in the present context might yield different concepts of levels of organization for each different role (R1) to (R3). While it helps to deflate the problem, the pluralistic strategy is objectionable for sacrificing the unity of the concept and with it the linkages between its diverse roles. In the case of levels of organization, these linkages—such as between compositional and causal levels—are some of the most interesting and rich aspects of the problem area. A further limitation of the pluralistic strategy, as stated, is that it assumes that the roles are all equally valid or important, rather than being subject to revision in light of the conceptual and empirical development of an account of levels.

Once we ascertain the reasons why (R1) to (R3) are dissociable, a different strategy presents itself. Broadly speaking, the main reason has to do with a common feature of evolved complex systems, which is the decoupling between structure and function, or between the intrinsic properties of a thing and the activities it participates in. If this is the case, there are better prospects for ordering things into levels if we refrain from considering all kinds of structures and activities at once. Instead, the strategy would be to partition a system into levels *relative to* a theoretical perspective or to one kind of causal process. This "decomposition under a process" includes only functions that align in contributing to the process and includes only the structural parts that perform those functions. I show how this might work in section 6.5 for the process of developmental evolution. In the perspectival or process-relative approach, a pluralistic splitting occurs between perspectives or kinds of processes rather than between the roles (R1) to (R3), which are maintained across processes or perspectives on levels.

While this strategy can reduce the dissociation between roles, it only goes so far. The further step is to take a constructive rather than descriptive approach to levels. Instead of treating each role that scientists and philosophers have assigned to the concept as a static target, these roles are allowed to change and to be only partially satisfied. The desirability of this stance derives from a sense that the concept of levels of organization has been overburdened with roles of great scientific and metaphysical significance, even though work on the topic arguably hasn't delivered the resources commensurate with this burden. In view of this situation, a constructive approach to levels pursues the tasks (R1) to (R3) as far as the landscape of the problem actually affords, in order to find the most "stable conformation" addressing all of (R1) to (R3).

6.3 Compositional Levels and Structure–Function Dissociation

One of the major obstacles to formulating a general account of levels that satisfies (R1) to (R3) is the following: for the entities that theorists would like to place into levels, their structure and their functioning often do not covary. The same structure can perform multiple functions, and the same function can be performed by multiple structures. Given the additional premise that structure and function are both important for representations of biological hierarchy, we have the situation that structural aspects will sometimes place an entity at one level while functional aspects place it at a different level. This creates a problem, because if the same entity is at multiple levels, then the inferences we want to make from level placements will become indistinct and confused. In this section, I illustrate the above argument by briefly outlining some of the limitations of mainstream accounts of levels based on structure, function, and combinations of the two.

6.3.1 Structural Levels

Most existing thought on (R1) is guided by the idea that certain structural types of objects identified by different sciences stand in orderly stepwise composition relationships. A classic expression of this idea can be found in Oppenheim and Putnam's (1958) "Unity of Science as a Working Hypothesis" (see Brooks, 2017). Here the aim is to map a hierarchy of levels that enables stepwise "micro-reductions" of things at one level (l_i) to things at the next lower level (l_{i-1}). From the aim of securing stepwise micro-reductions, Oppenheim and Putnam extract a number of "conditions of adequacy" for a theory of levels. The most important of these in the present context is the following: "(4) Any thing of any level except the lowest must possess a decomposition into things belonging to the next lower level" (Oppenheim & Putnam, 1958, p. 9). I will refer to this thesis as "type composition," by analogy to "type identity":

Type Composition: objects of type T_i at level l_i are composed exclusively of objects of type T_{i-1} at level l_{i-1} , unless l_i is the lowest level of objects.

Molecules at the molecular level are entirely composed of atoms at the atomic level. Atoms are entirely composed of elementary particles, which are perhaps not further decomposable. Along with this claim about types, Oppenheim and Putnam (1958) make the following claim about individuals: "Any whole which possesses a decomposition into parts all of which are on a given level, will be counted as also belonging to that level. Thus each level includes all higher levels" (p. 10). The idea that one and the same object can be identified at the level

appropriate to its kind, as well as at each lower level, implies that the object is identical to the set of its components. This thesis is known as “token identity”:

Token Identity: for every object x at level l_i , there is an object y at level l_{i-1} such that x is identical to y , unless l_i is the lowest level of objects.

Oppenheim and Putnam claim that these two conditions—type composition and token identity—are satisfied in the following empirical levels: elementary particles, atoms, molecules, cells, (multicellular) living things, and social groups.

Both type composition and token identity are problematic when viewed in light of straightforward assumptions about composition and identity in biological systems. The problem with type composition is that most objects above the level of molecules have components from multiple lower levels and not just from the immediately adjacent lower level. By analogy to multiple realizability, the systems studied by biology are characterized by “multiple type composition”: their components can belong to different structural levels due to their belonging to different types. For example, assuming Oppenheim and Putnam’s empirical levels, cells are composed of molecules but also of atoms and ions that are not components of molecules. Multicellular organisms are composed of ions, atoms, and molecules, and these need not be parts of cells (for example, in interstitial fluids and extracellular matrix). Social groups of animals can be composed of multicellular and single-celled organisms in symbiotic relationships. In short, type composition will fail whenever the same type of component can exist at many levels in a higher-level system. The most general reason why multiple type composition occurs is that, above the level of macromolecules, the entities of interest to science are typically individuated, at least in part, by their modes of functioning, rather than by their material composition. In order to be part of a functioning system, it is not necessary that a component belong to a particular structural level, such as the next lower level, but only that it function in a certain way within the system.

The problem with token identity is that biological systems and sets of their components tend to have different conditions of individuation and persistence. Sets are individuated extensionally, so that sets are the same when they have the same members. But cells, organisms, and social groups can gain and lose parts while still remaining the same. Further, it is often not possible to individuate a higher-level entity starting from lower levels of organization. When we examine scientific descriptions of “the same” object at different levels, we find that lower levels include more parts and more detail, some of which is irrelevant for the aspect of functioning that characterizes the higher-level object. In such cases, the higher-level object cannot be identified with the sets of parts we can pick out using the descriptive resources of lower levels (DiFrisco, 2018).

These problems feed into the same core difficulty for structural approaches to compositional levels. If we say that l_{i+1} entities are composed of l_i entities, we at once include too much and too little in l_{i+1} : too much, because some parts from l_i may not be functional parts of l_{i+1} ; too little, because parts from l_{i-1} and l_{i-2} may be functional parts of l_{i+1} . Purely structural approaches to compositional levels yield causally irrelevant and arbitrary objects, such as organisms without their noncellularized parts or organisms whose parts include physical entities that are too minute to actually affect their functioning.

A hierarchy of structural types defined without reference to functioning inevitably exhibits a divergence between compositional levels (R1) and causal levels (R2). Will the

situation be improved if we define compositional levels starting from function, process, and causal interaction?

6.3.2 Functional Levels

The notion of function as it appears in the structure–function dialectic of biology can be understood in multiple ways (Brigandt, 2017; Gillett, 2013b; Griesemer, 2006; Love, 2007). The function of an entity can refer to its effects, relations, roles, goals, or outcomes, but it can also refer to its functioning—to activities, processes, or behaviors. Effect functions have been a central analytical category in traditional evolutionary theorizing about levels, for example, in work on levels of selection (Lewontin, 1970; Okasha, 2006) and replicator–interactor levels (Hull, 1980; Salthe, 1985). Activity functions or processes have more recently begun to play a more central role in evolutionary theorizing from a developmental perspective (Amundson, 2005; Griesemer, 2000, 2006; Jaeger, 2019; Jaeger & Monk, 2014; Love, 2007), but without yet issuing in an account of *levels* of developmental evolution.

The main rationale for a shift from effect function to activity function is based on the idea that understanding evolution requires “opening the black box” of developmental processes and examining their causal structure. As Griesemer (2006, 347) points out, analyses based on effect functions “depend on tacit reference to a process in which a goal is served, but they do not offer an account of those processes.” This is why effect-functional analyses of levels are typically uninformative until they are mapped onto levels of structure or process, which provide the structures and causes that *realize* the effects (Griesemer, 2005). To say that l_i is a level of selection if entities at l_i engage in fitness-affecting interactions (Okasha, 2006) does not tell us which entities are at that level, nor does it describe the processes and interactions that affect fitness at that level. It simply gives an extra condition that some entities—whatever they are—must satisfy in order for some occurrence—whatever it is—to result in selection.

For now, I will only consider activity-functional analyses as candidate accounts of levels. There are two broad kinds of activity-functional approaches to levels: one classifies objects and their functioning or activity into levels, and the other only classifies functionings or activities themselves into levels. Probably the most well developed of the first form is Craver’s (2007, 2015) account of levels of mechanisms. This account is concerned with understanding levels in the context of mechanistic explanation. The basic idea is that a component and its activity are at a lower level than a mechanism and its activity if these entity–activity pairs stand in two relations: a part–whole relation and additionally a relation of “mutual manipulability.” For the part and whole to be mutually manipulable means that in intervening on the component or activity, one can observe changes in the mechanism and its activity and vice versa. As for the same-level relation, components and their activities are at the same level if they are manipulable parts of the same mechanism and neither is part of the other (Craver, 2007, p. 192).

By substituting a causal relevance criterion for structural types, the mechanistic view allows classification into levels without appeal to type composition and provides a way of limiting the lower-level components to only the causally relevant ones.¹ However, the advantages of abandoning structural types for understanding interlevel relations come at the expense of a well-defined *intralevel* relation (for detailed argument, see DiFrisco, 2017; Eronen, 2013, 2015). This issue has been addressed by restricting the scope of levels

to local token mechanisms and denying that the intralevel relation is transitive and thus that it has much significance (Craver, 2015). Without a stable intralevel relation and without types, however, there is little possibility of reaching generalizations about composition (R1), causation (C2), or other qualitative features (R3).²

A second functional approach is to shift from placing entities at levels and instead to focus on hierarchical relations between dynamical categories—processes, activities, behaviors, functionings, events, and so on (Allen & Starr, 1982; Baedke & McManus, 2018; DiFrisco, 2017; Goodwin, 1963; O'Neill et al., 1986; Seibt, 2014). In DiFrisco (2017), I argued that this is the most generally reliable way of satisfying (R2), but this required abandoning typological and compositional criteria for level placements in favor of a dynamical one—namely, time scale. Like the mechanistic account, this sort of approach escapes the problems with Oppenheim and Putnam's (1958) scheme, but without losing a well-defined intralevel relation, since sameness of level is simply construed as similarity of time scale within an interactive context. As a consequence of the latter, time scale hierarchies of processes need not be restricted to tokens and to highly local contexts and thus give a more general answer to (R2). However, this approach only advances toward (R2) by setting aside (R1) altogether and also to some extent (R3). This approach does not help us to identify and describe the variety of noncausal “making-up” relations between types—neither between types of objects, *nor* between types of processes. Accordingly, this second functionalist approach fits into the pluralist strategy where different accounts are developed specifically for different roles (R1) to (R3) of levels of organization. In keeping with the limitations of the pluralist strategy noted earlier, we gain precision but lose the important linkages between the different roles (i.e., between composition, causation, and generalization over types).

6.3.3 Hybrid Structural–Functional Levels and Cluster Kinds

A different line of approach to levels combines structure and function concepts. Wimsatt's (1976, 2007) writings on levels of organization target each of (R1) to (R3) (among other tasks) while avoiding the above problems with Oppenheim and Putnam's (1958) structural hierarchy as well as functionalist hierarchies. He does this by reinterpreting type composition (R1) and causal levels (R2) as providing generally reliable *characterizations*, as opposed to *definitions* in terms of necessary and sufficient conditions for being at a level (Wimsatt, 2007, p. 204). This redirects attention away from finding definitions that avoid counterexamples and toward characterizing the many empirical linkages between composition, scale, causation, and scientific explanation. Although it is not explicitly conceptualized as such, Wimsatt's levels can be viewed as “cluster kinds,” where membership is determined not by essential properties but by having any of a number of properties that tend to cluster together. Both structural and functional aspects can be included in the cluster of characteristic features of a level. The flexibility of this conception of levels allows for wide-ranging and hybrid characterizations like the following:

One thing is at a higher level than something else if things of the first type *are composed of* things of the second type [(R1)], and at the same level with those things it interacts most strongly or frequently with or is capable of replacing in a variety of causal contexts [(R2)]. (Wimsatt, 1976, p. 215)

The theories at different levels might be thought of as sieves of different sizes, which sift out entities of the appropriate size and dynamical characteristics [(R2)]. ... If the entities at a given level are

clustered relatively closely together (in terms of size, or some other generalized distance measure in a phase space of their properties) it seems plausible to characterize a level as a *local maximum of predictability and regularity* [(R3)]. (Wimsatt, 1976, pp. 237–238)

These claims can be illustrated with many rich examples from the sciences (Wimsatt, 1976, 2007). The major advantage of adopting a nonessentialist view of levels is that one can capture interesting linkages between different features of levels without worrying about exceptions or counterexamples. Salthe (1985) offers another framework on levels of this same kind.

Understanding levels in terms of property clusters can also provide a straightforward way of comparing different empirical levels as to their degree of uniformity. When the properties of the cluster closely covary, there are highly uniform levels. These would include the atomic, molecular, and perhaps the cellular—the most lawlike of biological levels. When the properties of the cluster only loosely covary, for reasons such as the decoupling of structure and function, then levels are less uniform and less “level-like.” Wimsatt (2007, p. 221) describes a situation where, as we ascend to systems with greater descriptive and interactional complexity, levels “break down” and are replaced by “perspectives” and “causal thickets.” Levels tend to break down above the cellular level, yielding to multiple perspectives on multicellular organisms and, higher still, the “bio-psychological thicket” of the human brain, social institutions, and culture (Wimsatt, 2007, 233).

One way of explicating the idea of a “breakdown” of levels is to say that, as structure and function get decoupled in certain complex systems, level placement becomes *nondiscrete*. Discreteness of level placement means that the same thing is not at different levels in the same hierarchy. Discreteness is commonly assumed to be a necessary feature of levels (Bechtel, 2012; Potochnik & McGill, 2012), because without it, placement at a level becomes noncontrastive and uninformative. The discreteness requirement will be harder to meet as properties from a cluster covary more loosely. This is because membership in cluster kinds or levels tends to be quite permissive: any property in the cluster is sufficient, and none is individually necessary, for membership in the kind. Accordingly, an entity can have a structural property that is sufficient to place it at one level, while also having a functional property that is sufficient to place it at a different level. For example, colonies of eusocial insects are groups of metazoans, but their behavior, metabolic scaling, and other features are quite similar to that of solitary organisms (Hou et al., 2010). Should they be counted as belonging to the organism level or the level of groups or populations of organisms?

One could decrease the occurrence of nondiscreteness by stipulating that membership in a level requires surpassing a certain *threshold* of properties from a cluster. But this move would undercut the primary motivation for shifting to cluster concepts from essential properties. In setting a threshold of clustered properties for membership in a level, the risk is that many individuals would fail to surpass the threshold at all. Rather than being placed at *multiple* levels, they would be placed at *no* level. These level-less individuals would be excluded from generalizations (R3) and causal inferences (R2) about levels. Another possibility is that entities failing to surpass the threshold would be counted not as individuals at the focal level (e.g., a multicellular organism) but as *groups* of individuals at the next lower level (e.g., a collection of cells).³ This reconceptualization may be appropriate when the individual really is more like a group of lower-level entities—for example, slime molds during the foraging phase of the life cycle. But such borderline cases of multicellularity—slime molds and obligately eusocial insect colonies—are precisely cases that do not easily

fit into discrete levels of “cells” or “organisms.” In a sense, *any* classification into one or the other levels is misleading. Hence, it seems that access to the wide diversity of generalizations about levels is only granted at the cost of nondiscrete or misleading level placements. When level placements are nondiscrete, it is difficult to single out the appropriate units of generalization to determine which phenomena instantiate the predictions and regularities, and thus it is difficult to apply the levels scheme in specific cases. When level placements are misleading, the generalizations and inferences may do more harm than good (see Potochnik, this volume).

Wimsatt’s framework may capture the most that a monistic approach can say about levels of organization viewed as robust points of convergence across all scientific domains at once. In order to gain in precision about placements at higher levels without losing what is interesting about levels, one has to move from a general discussion of levels to a specific scientific contextualization. I propose to do this in section 6.5 in examining levels of developmental evolution. This move involves the following reorientation: instead of looking for unique levels placements that hold across diverse scientific perspectives, we consider only one perspective tracking one kind of causal process (e.g., metabolism, development, evolution) and decompose systems into levels relative to that perspective or process. In this approach, it should be the case that levels break down at higher scales than before, and complex entities such as organisms or traits can be ordered into levels without the same ambiguities native to *general* levels of organization.

6.4 Decomposition under a Process, Constitution, and Levels

From the preceding discussion of compositional levels, we can see how the nature of scientific composition constrains how levels of organization should be understood. Functional and Wimsattian approaches to levels depart from structural approaches on the basis of a different picture of scientific composition. They recognize that the criteria of individuation used in different sciences and at different scales pick out objects that do not necessarily stand in neat compositional relationships to one another. I will refer to this phenomenon as *relativistic composition*. Relativistic composition undermines the structuralist theses of type composition and token identity found in Oppenheim and Putnam’s (1958) framework. More generally, relativistic composition creates the following challenge for accounts of compositional levels: how can a hierarchy include the entities that are targeted in actual scientific explanations, while also putting those very entities together into some form of unifying compositional relationship? This section will explore how the notions of decomposition under a process and constitution relationships between processes can address this challenge.

To start, it will be helpful to consider why relativistic composition occurs in science. Two key papers by Kauffman (1971) and Wimsatt (1972) develop the idea that different decompositions of the same system result from our bringing different *perspectives* to scientific investigation. From here we get the rich notion of *descriptive complexity*. The descriptive complexity of a system is the degree to which different perspectival decompositions yield nonoverlapping sets of parts. In biology, perhaps the best examples of descriptively complex systems are organisms and phenotypic traits, and these are also the entities for which levels start to break down. In the case of organisms, recent work on biological individuality

has generally aligned in showing that there are irreducibly multiple, partially overlapping boundaries we can draw around organisms and that the different individuals that have these different boundaries figure into different perspectives and styles of explanation. For example, ecological perspectives tend to be more inclusive than evolutionary ones: in a given community of symbionts, there might be one large cohesive ecological individual but many distinct evolutionary individuals (Clarke, 2016; see DiFrisco, 2019).

As the language of “perspectives” suggests, relativistic composition is partly a consequence of the plurality of aims, interests, and cognitive strategies that we bring to bear on the world. But relativistic composition is also a reflection of the way the natural world is. Ecological perspectives differ from evolutionary perspectives not only because they have different investigative aims but also because they track different kinds of natural processes and discover different regularities and patterns. Importantly, these different processes have different participants. Animals together with their symbiotic microbes might jointly participate in the same processes of growth, migration, predation, and adaptation but in different processes of reproduction and developmental differentiation. If we ask whether the “animal plus microbes” system is on the organism level without specifying a reference process, the answer is likely to be ambiguous between decompositions of the system under different processes.

The idea of a causal process as an individuator of objects has been proposed in biology before.⁴ In examining the individuation of organisms, Laubichler and Wagner (2000) maintain that “functionally relevant biological objects can be defined only within the context of a specific biological process” (p. 293). von Dassow and Munro (1999), in discussing the notion of modularity in evo-devo, write,

The way we conceptualize module and mechanism depends both on the reference process (on whether we are interested in morphogenesis or epigenesis, or in the evolutionary process itself) and on whether we are thinking analytically or synthetically. The first arises because we are talking about disjunct types of process in which biological entities participate differently; the second selects our operational criteria. The practical consequence of both is merely that biologists must be careful not to assume any particular correspondence between units that emerge from each perspective. (p. 308)

A classic example of a trait that is not a unit of developmental processes is the human chin (Gould & Lewontin, 1979; Wagner, 2014), which is a by-product of adjacent modular growth fields. Yet the chin could be a unit relative to a process of sexual selection. This sort of process relativity vexes attempts to identify “the” module and place it on a level relative to other entities.

In order to make the notion of decomposition under a process workable, it will be necessary to get clearer on what processes are. If biological entities are individuated by the processes they participate in, how are the processes individuated? A natural worry should be addressed from the start, which is that processes will have to be individuated by their participants, rendering the individuation condition objectionably circular. This type of worry is based on an abstract metaphysical picture of individuation rather than the messy world of empirical science (see Bueno et al., 2018). Metaphysically, individuation is a determination relation: it is irreflexive, asymmetric, and possibly transitive (Lowe, 2003). The asymmetry condition means that if x individuates y , then y cannot also be what individuates x . It is not difficult to see how, given asymmetry and irreflexivity, individuation is subject to a potential infinite regress in which, for any individuator x , one must ask what individuates x . The situation is analogous to the problem of regress in epistemic justification.

According to foundationalist epistemologies, chains of epistemic justification must terminate in “self-justifying” or “self-evident” principles, reasons, or perceptual givens. A similar foundationalism about individuation can be found among metaphysicians such as Lowe (2003), who maintains that chains of dependency in individuation must terminate in “self-individuating” things, thus violating irreflexivity.

However, the most plausible epistemologies of science are antifoundationalist, and antifoundationalism about individuation is also the more appropriate stance for understanding the workings of science. Scientific investigation starts from objects, events, and processes that are reasonably thought to be suitably individualized and revises the relative boundaries in a relational and iterative fashion as knowledge about the world grows. Some elements are held fixed during the revision of others, but ultimately all are revisable. This situation does not violate the irreflexivity or asymmetry of individuation; instead, individuation can be reciprocal if it is iteratively operating between entities that are *roughly* the same but with progressively revised boundaries. On this picture, processes can have important individuating roles without being foundational or self-individuating. An initial characterization may be enough to get an operational handle on processes, which would then be subject to further revision and refinement.

What are processes, then? In *The Strategy of the Genes*, Waddington (1957) wrote that “to provide anything like an adequate picture of a living thing, one has to consider it as affected by at least three different types of temporal change, all going on simultaneously and continuously” (p. 6). The three processes he identified were evolution, development, and metabolism. These processes are distinct because they have different participants, instantiate different regularities or patterns, and operate at different time scales. Finer-grained subprocesses can be distinguished within these—for example, selection and speciation, morphogenesis and growth, catabolism and homeostasis, with still finer distinctions within these. The status of these categories as *processes* is reflected in the fact that they involve patterns of change not only in the properties of things but also in the identities of things and components through time. The primary biological processes identified by Waddington are also supposed to be causal rather than epiphenomenal. This feature of processes is explicated in Salmon’s (1984) process theory of causation in terms of their capacity to transmit “marks” across spacetime. Drawing on Bertrand Russell’s notion of a “causal line,” Salmon maintained that causal processes are “self-determined”: they transmit their own uniformities of qualitative and structural features, and they exhibit regularities that allow inferences from what is happening during one part of the process to what is happening during another part of the process (Salmon, 1984, pp. 144–145).⁵ Beyond these general features, a useful kind of further precision on the individuation of processes will likely have to come from consideration of the specific *sort* of process one is theorizing about.

To get compositional levels from processes, one needs a working understanding of “vertical” relations between processes as well as a notion of components participating in processes. The vertical relation should be a form of constitution rather than identity, because processes that are identical are at the same level. The central processes I focus on are evolution and development. In evolutionary developmental biology, theorists will sometimes say that evolution should be viewed as being, constitutively, the evolution of development (e.g., Gilbert et al., 1996, p. 362; Amundson, 2005). This is supposed to contrast with narrower views of evolution, such as Dobzhansky’s view that evolution is change in

allele frequencies. But what does it mean to say that evolution is *constituted by* development? Three aspects can be highlighted.

First, it means that evolution cannot change without development changing. If we take development in an inclusive sense that includes genotypic and phenotypic changes, there is no evolutionary change without change in development.⁶ Second, although processes of development and evolution occur at different time scales, they occur during the same time intervals. At least for organisms that are thought to undergo development (eukaryotes) (Minelli, 2011), there is no process of evolution that occurs at a time and place where development does not also occur. Third, the entities that participate in evolution (primarily populations) are composed of the entities that participate in development (primarily organisms). Note, however, that development may include parts that are not part of an evolutionary process. Anything that is not heritable or that does not impact future generations, such as certain acquired somatic defects or achievements, is not taken up into the evolution of populations.

Starting from this example, a relation of process constitution can be formulated as follows:

Process constitution: process x is constituted by process(es) y_n iff: (1) x cannot change without y_n changing, but y_n can change without x changing, (2) x and y_n occur in the same spatial region and during the same time interval, and (3) the entities that participate in x are either exhaustively composed of the entities that participate in y_n , or they are composed of a subset of the entities that participate in y_n .

In most cases, the constitution base of a biological process x will be several qualitatively distinct processes (y_n) rather than one. A process y_1 that is only part of the full constitution base y_n can be termed a “partial constituent” of x .

There are several things to note about the three conditions on process constitution. Condition (1) is close to the notion of supervenience except in two respects. First, the relata are causal processes rather than properties. Second, the constituting process must be able to change without the constituted process changing. If constituting and constituted processes each supervened on the other, then they would be identical under the principle of the identity of indiscernibles. Normally, property supervenience is formulated in a way that is compatible with the properties being identical, but here the aim is to build in a distinction between constitution and identity for an account of levels. Condition (2) for process constitution excludes “horizontal” or diachronic determination relations from counting as cases of constitution. Condition (3) ensures that the constitution relation is anchored in the right region of space. But note that it is consistent with the phenomenon of “part loss” across scales. Development can include parts and events that are not part of an evolutionary process. The same is true for molecular metabolic processes and developmental process and perhaps also for neurophysiological processes and mental processes. Conditions (1) and (3) reflect the same underlying relationship between lower and higher levels: the lower level typically includes more than the higher level. This can be a consequence of the fact that higher-level perspectives and processes select only certain parts from the detail of the lower level but also because the scalar differences between levels are such that lower-level effects are not strong enough to make a difference at the higher level.

The above notion of constitution yields a straightforward *interlevel* relation for processes:

Interlevel (processes): two processes are at different levels in the same hierarchy iff they stand in a constitution relationship. Constituting processes are at a lower level than constituted processes.

Note that this interlevel relation, combined with condition (1) on process constitution, generates the expectation that lower-level processes will have shorter time scales than higher-level processes (DiFrisco, 2017). If l_i can only change when l_{i-1} is changing, but l_{i-1} can change without l_i changing, then the regular changes in l_{i-1} should be occurring at a faster rate.

From here we can put forward the following interlevel relation for *entities*:

Interlevel (entities): two entities are at different levels in the same hierarchy iff there is a constitution (not identity) relation between the processes they participate in. Participants in constituting processes are at a lower level than participants in constituted processes.

An organism is at a different level than its population because they figure into distinct processes (e.g., development and evolution), and these processes are related by constitution. Since development is the constituting process, the organism is at a lower level than the population. Note that process constitution gives levels a restricted scope. There is no constitutive relation between population processes and climate processes in an ecosystem (although there could certainly be causal relations between them), and so populations and climate processes are neither on the same level nor on different levels within the same hierarchy.

To formulate an *intralevel* relation, we can start from the notion of partial constitution: two processes are on the same level if they are partial constituents of the same overarching process. This should not be viewed as a necessary condition, because in many cases, we want to put processes on the same level without there being a relevant overarching process—for example, two processes of evolution or selection in different populations. Likewise, we may want to put two processes on the same level when they are not direct constituents of the same process but only constituents of constituents of the same process. This would be the case for spatially separated cellular-level processes that are constituents of different tissue- or organ-level processes that are constituents of the same metabolic or developmental process. The intralevel relation for processes should therefore accommodate this sort of flexibility:

Intralevel (processes): two processes are at the same level in the same hierarchy iff (1) neither process constitutes the other and either (2) they are partial constituents (y_1 and y_2 of y_n) of the same process (x), or (3) they are sufficiently similar in some relevant feature among the cluster of characteristic intralevel features.

Characteristic features of intralevel processes include the broad Wimsattian variety: similarity in structure, function, dynamics, or scale or interacting more strongly or frequently with each other.

The same approach can be applied to the intralevel relation for entities. To start, two entities are at the same level in the same hierarchy if neither is part of the other and if they participate in processes that are partial constituents of the same overarching process. Hence, an organism is on the same level as another organism because they both participate in processes (development) that are partial constituents of the same overarching process (evolution), and neither is part of the other. Without further qualification, however, this intralevel relation will run into similar difficulties as Craver's (2007) levels of mechanisms whenever we consider multiple partitions of constituency (see DiFrisco, 2017; Eronen,

2013, 2015). Again, the most promising way forward will be to rely on a nonessentialistic “cluster” interpretation of the intralevel relation:

Intralevel (entities): two entities are at the same level in the same hierarchy iff (1) neither is part of the other, and either (2) they participate in processes that are partial constituents (y_1 and y_2 of y_n) of the same overarching process (x), or (3) they are sufficiently similar in some relevant feature among the cluster of characteristic intralevel features.

The “sufficiently similar” in conditions (3) no doubt introduces some indeterminacy into intralevel placements for entities and processes. This can be filled in for different contexts of inquiry that invoke levels. Qualitative similarity and belonging to the same type will be more important intralevel criteria for (R3) contexts—especially for generalization, comparison, and inference across systems that are not causally interacting. For example, it may be useful to invoke levels in comparative studies of major transitions in individuality between two populations that never interact with each other. In such cases, relevant similarities can ground statements, inferences, or models about a “group level” or “colony level” that includes both populations at once. By contrast, similarity in scale as well as interacting more strongly or frequently will be more important criteria for (R2) contexts, when the concern is to discover the causal structure of systems whose parts are potential interactants. While these kinds of qualifications may help reduce some of the ambiguity of same-level placements, some ambiguities will remain. There is likely no other way to capture all of the interesting cases where we want to place entities at the same level than tolerating some degree of nondiscreteness.⁷

This framework for understanding levels leaves a number of issues open. Among these is what it means to “participate in a process.” The notion of dispositional properties or conditional powers will probably be important here (see Gillett, 2013a). For now, I note some points in favor of this type of levels scheme.

- By connecting compositional levels directly to the category of processes, we make composition sensitive to causal relevance, which cannot be done with the standard object–property ontology of levels. Accordingly, unlike Oppenheim and Putnam’s (1958) structuralist account, this levels scheme is consistent with “multiple type composition” in the sciences and thus gives us a better grasp of composition relations between types (R1).
- As a contextual specification of Wimsatt’s (1976, 2007) general levels of organization, the restriction to a single overarching process reduces (without eliminating) the amount of ambiguity in levels placements and nondiscreteness of levels. As a result, one can expect that “levels break down” at higher scales than in the general scheme, and it should be easier to instantiate regularities and predictions about the focal process at higher levels (see section 6.5).
- Unlike Craver’s (2007, 2015) levels of mechanisms, there is a stable intralevel relation, although it is based on a cluster of characteristics. In addition, the items at levels need not be tokens and need not figure into mechanistic explanations specifically (e.g., whole-organism or population-level processes).
- Including processes and their constituency relations in the account of compositional levels provides a categorially richer picture of levels of organization than is available from structural hierarchies. Of particular interest is that we can represent processes themselves as units

of generalization, or as maxima of regularity and predictability, rather than attributing this role to entities only (R3). This is important when the same process has a shifting participant base, such that the regularity is to be found in the process rather than the entities that transiently participate in it. This phenomenon is common in comparative developmental biology.

In order to put these ideas to work, I want to now take a more detailed look at a specific scientific contextualization of levels in evolutionary developmental biology.

6.5 Levels of Developmental Evolution

“Developmental evolution” refers to the confluence of two causal processes, one constituting and one constituted. This confluence involves a two-way filter of each process from the perspective of the other. On the one hand, development is viewed from evolutionary perspective, which filters out constituents of development that are not heritable and that do not vary. On the other hand, evolution is viewed from a developmental perspective, which filters out evolutionary effects that are not caused by development. That evolution has nondevelopmental causes is compatible with the thesis that evolution is constituted by change in development. According to Van Valen’s (1973) pithy formula, “evolution is the control of development by ecology.” Ecology has controlling influences, but development is what is controlled—that is, ecological effects on evolution are manifested in development as the substrate of evolutionary change.⁸

In fact, the individuation of these processes is not precise and fixed but is a dynamic element in the ongoing growth of evolutionary and developmental biology. This is especially true of development, since developmental biology is not characterized by an overarching theory describing a unified process of “development” but rather by families of diverse approaches to *aspects* of development (Love, 2015; see Minelli & Pradeu, 2014, and essays therein). These aspects are subprocesses within development, such as transcriptional regulation, differentiation, cellular processes, growth, tissue mechanics, and so on. “Development” can be viewed as the complex embedding process, of which these subprocesses are partial aspects. Since this process of development has mobile boundaries and a yet-unresolved structure, what it means to “filter” evolution through a developmental perspective will change as developmental biology changes. It is important to point out, however, that this broad sense of development differs from what is more often referred to as development, which is *early* development, embryogenesis, and morphogenesis of major characters. The narrow process of development may include major causes of evolutionary change, but only the wider process can be what constitutes evolutionary change.

6.5.1 Levels and Variational Independence

Researchers in evo-devo sometimes refer to general levels of organization (i.e., molecules, cells, tissues, organs, organisms), but more often, what is at stake is levels of organization decomposed under the process of developmental evolution. These more restricted levels do not include everything that exists in the organism but just the main parts that have causal or constitutive relevance for the process of developmental evolution (see table 6.1).

Let us now map these items onto the levels scheme from the previous section. Starting with interlevel relations, note that, in the right column of table 6.1, the relation between

Table 6.1
A schematic catalogue of the levels of developmental evolution

Entity level	Process level
population	evolution
organism	development, ontogenesis
<i>character</i>	development
cells/tissues	<i>morphogenesis</i>
<i>gene network</i>	regulatory interactions, signaling, transcriptional state specification
<i>gene</i>	gene expression and regulation

Note: Categories emphasized in bold italics are those that possess a significant degree of variational independence (see text and table 6.2).

lower and higher processes is one of constitution (or partial constitution) without identity. As for intralevel relations, different processes, such as processes of gene expression, can be on the same level by being constituents of the same overarching process, such as a complex regulatory cascade or intercellular signaling. However, most processes of gene expression in a developing organism are not direct constituents of the same individual process. They can be placed on the same level, if one likes, on the basis of their close similarity in many of the characteristic intralevel features (structure, function, dynamics, scale, and interacting more strongly or frequently with each other than with other processes). The same intralevel relation can be derived for the other process levels.

In the left column, the entities are at different levels because they participate in processes that are related by (partial) constitution. They are also at different levels because they compose one another, given that one of the conditions on process constitution is that the processes have participants that are related compositionally. But the strategy here is not to *lead* with a notion of composition, instead relying on causal processes to *select* the functionally relevant composition relations from more inclusive levels of organization. This is why the compositional relations between entity levels are not exhaustive (e.g., cells are composed of more than just gene networks). Entities like genes are on the same level when they participate in processes (gene expression) that are partial constituents of the same overarching process (e.g., transcriptional regulation, signal transduction). Again, however, most activities of gene expression in a developing organism are not direct constituents of the same regulatory process but are separated by intermediary processes. Genes can then be placed on the same level on the basis of their similarity in the characteristic intralevel features. Again, the same analysis of inter- and intralevel relations can be repeated for the other entities in the left column.⁹

More entities and processes can be added to the hierarchy depending on the grain of analysis. In general contexts of discussion, however, workers in evo-devo often work with *fewer* levels: primarily, genes, gene networks, morphogenetic processes, and phenotypic characters (see table 6.2). The reason why these items are singled out at levels is that they are considered to have the greatest influence on the process of developmental evolution—they are the primary “levels” at which the process determines its course. To participate in an evolutionary process, it is necessary that some item possess heritable variation, so that it can reliably reappear over generations. To be a “unit” or “module” of heritable variation, the item must vary independently or “quasi-independently” of other items. The condition

Table 6.2

Description of variational independence across levels

Level	Variational independence
Character level	<ul style="list-style-type: none"> • Different processes can cause the same (homologous) character. • The same processes can cause different characters.
Process level	<ul style="list-style-type: none"> • Different networks can cause the same morphogenetic process. • The same networks can cause different morphogenetic processes.
Network level	<ul style="list-style-type: none"> • The regulatory topology of a network is not uniquely specified by its component genes, so the same genes can compose different networks. • Different individual genes can have the same functional roles in a gene regulatory network, so the same networks can have different genetic components.
Genetic level	<ul style="list-style-type: none"> • Individual genes are paradigmatic units of heritable variation, varying independently of variations at higher levels.

of *variational independence* captures what it means for something to be a functioning unit of developmental evolution. Brigandt (2007) proposes that variational independence is what makes a body part a distinct character in developmental evolution. The same condition of variational independence (or “quasi-independence”) can be used for understanding levels of developmental evolution if it is combined with the conditions on levels from the previous section.¹⁰

Variational levels of developmental evolution: some class of items constitutes a level of developmental evolution iff: (1) that class varies (quasi-)independently of other classes of items, and (2) the classes are at different levels in the same process hierarchy (see “inter-level (processes)” and “interlevel (entities)” above).

The variational independence of phenotypic characters from the morphogenetic processes that produce them has been recorded observationally since the early days of embryology (see Scholtz, 2005, for examples). A well-studied example is the segmented anteroposterior axis of insects, which is a conserved character despite its being produced by different segmentation processes in different insect groups. In short-germ segmentation (found in more basal insect orders), segments are specified sequentially from anterior to posterior. In long-germ segmentation (found in more derived holometabolous insects), segments are specified simultaneously by subdivision of the blastoderm (Clark et al., 2019; Liu & Kaufman, 2005).

The variational independence of morphogenetic processes from the networks that cause them is increasingly coming to be appreciated as dynamical modeling of morphogenesis is incorporated into the research methods of evo-devo (DiFrisco & Jaeger, 2019; Jaeger, 2019; Jaeger & Monk, 2014; von Dassow & Munro, 1999). An example of the same network underlying different processes again comes from studies of insect segmentation. The same gap gene network produces different segmentation phenotypes in fruit flies and scuttle flies due to time-variable maternal inputs, differences in regulatory strengths within the network, and the fact that different subnetworks are in a critical state in the two groups (Jaeger & Monk, 2014; Verd et al., 2019). An example of different networks underlying the same morphogenetic process can be found in the vertebrate segmentation clock (Krol et al., 2011). Vertebrae develop out of segmented precursors in the mesoderm known as somites. Somitogenesis is described by the “clock and wavefront” model (Cooke & Zeeman, 1976): somites are produced by the interaction between oscillating waves of gene expression

(clock) and a mechanism that halts the waves in a periodic fashion (wavefront). Comparative studies have revealed that, even though the segmentation process is conserved across all vertebrates, there are substantially different networks with different individual genes in distant vertebrate groups (mouse, chicken, and zebrafish) (Krol et al., 2011).

The variational independence of gene networks from individual genes can be expressed in terms of dissociation between gene functioning in networks (regulatory role) and gene structure (base pair sequence). Structurally different genes can have the same functions, and significant amounts of functional redundancy from the genetic level to the network level are well documented. In the vertebrate segmentation clock, for example, the presence of many genes capable of producing the same kind of oscillatory behavior may have allowed genetic divergences to accumulate over evolutionary time (Krol et al., 2011). Likewise, the same genes can have different functions and acquire new functions with apparent ease in evolution (True & Carroll, 2002). Many key regulatory genes, such as genes from the *Notch* and *Wnt* families, are used and reused in completely different networks and developmental processes. So even though gene networks are entirely composed of individual genes, their identity is not determined by the structural identity of the component genes. Instead, it is the *interactions* between genes in a network, as well as the network's spatiotemporal and cell-biological context, that gives them causal specificity in the process of morphogenesis. Their status as crucial *units* of variational independence derives from the fact that, as Wagner (2014) writes, genes organized in networks “form a functional unit in which developmental causality is realized at the level of the network rather than at the level of the single gene” (p. 117). The move toward explaining development in terms of complex networks of interacting genes rather than individual genes has been one of the major breakthroughs of developmental genetics in the past decades (Peter & Davidson, 2015; Salazar-Ciudad & Jernvall, 2013; see DiFrisco & Jaeger, 2019).

6.5.2 Theoretical Roles for Levels of Developmental Evolution

How do the levels of developmental evolution map onto the three major roles (R1) to (R3) for levels distinguished earlier? On (R1), these levels identify general composition relationships under a dynamical aspect in which composition is relativized to a focal process. Not all components are placed into levels, so following a “constructive monist” approach to levels (see section 6.2), (R1) is partly sacrificed for the other roles.

On (R2), there is some truth to the general idea of stronger interactions within levels than between levels, but the process of development centrally involves *interlevel* causation (see Baedke, this volume; Green, this volume; Woodward, this volume). More important for (R2) is the notion of causal independence (see Woodward, this volume), which appears in this context as variational independence. There is a tension here between independence and levels, since constitution is a type of dependence relationship. How can higher-level things be causally independent if they are composed of, or constituted by, lower-level things? In many cases, the causal independence of higher-level variables can take the form of a summation or screening-off. For example, conditional upon the temperature of a sample of gas at thermal equilibrium, variations in the kinetic energies of its component molecules that are consistent with this temperature do not make a difference to its pressure (see Woodward, this volume). We have seen a strong form of causal independence in which the higher-level variable is robust under perturbations to the components and also possesses

greater generality. The segmentation clock in each vertebrate species is caused by a unique regulatory network and set of individual genes, so it is ultimately dependent on these factors. But these lower-level factors vary across taxonomic groups, whereas the morphogenetic process (somitogenesis) character (somites) and certain key signaling pathways (Wnt, FGF, Notch) do not. The development of somites is evolutionarily most stable at the “process level.” Causal explanations of somites in terms of the morphogenetic process therefore have greater generality than those in terms of the participant genes.

This leads directly into the role of generalizing over levels (R3). Discovering comparative generalizations is a crucial task in evo-devo because there are too many species to study individually. Levels, as depicted in table 6.1 and especially table 6.2, contribute to this task by demarcating stable bases of comparative generalization. Importantly, these levels include more than just genetic and network levels, although those levels have been the major focus of comparative evo-devo so far. The generalizability of causes of development at different levels is expressed in Salazar-Ciudad and Jernvall’s (2013) notion of a “causality horizon.” Essentially, the causality horizon between compared species is the lowest level at which the causes of a morphological feature are the same. Vertebrate somitogenesis has a *high* causality horizon—namely, the level of the morphogenetic process (oscillating clock and wavefront). Below the causality horizon, identifying the more fundamental cause of a phenotype in one species will not successfully predict the cause of a corresponding phenotype in another species (Salazar-Ciudad & Jernvall, 2013, p. 286). Accordingly, the causality horizon represents “the boundary of successful, or appropriate, reductionism in development” (Salazar-Ciudad & Jernvall, 2013, p. 286).

The causality horizon demarcates “maxima of regularity and predictability” (Wimsatt, 2007, p. 209) in developmental evolution (R3). That these maxima can be *processes* in addition to the standard compositional entities is an insight that becomes accessible by shifting from the frame from structural levels and general levels to decomposition under a specific causal process.

6.5.3 Beyond Levels of Selection and Replicator–Interactor Levels

I close this section by noting a few of the ways in which levels of developmental evolution represent a richer conceptualization of levels than existing evolutionary frameworks. There are no such frameworks that take a purely structural perspective, probably because structural frameworks would have difficulty accommodating selection for function. More standard frameworks are based on effect functions, such as levels of selection and the replicator–interactor hierarchy (for a classic, in-depth criticism of these frameworks, see Griesemer, 2005).

Much theorizing about evolution in biology and philosophy takes place in the hierarchical frame of levels of selection (Lloyd, 2017; Okasha, 2006). One issue with levels of selection as an ontological framework is that it presupposes a background notion of levels of organization that remains unanalyzed (Griesemer, 2005), and *general* levels of organization are probably too blunt an instrument for this role (Eronen & Ramsey, 2021). A more basic limitation is that selection is only a subprocess of evolution. Levels decomposed under the process of selection do not capture the sources and structures of variation, which are developmental and genetic, but only the *outcomes* of development. Accordingly, levels of selection alone are too limited to serve as the hierarchical framework for explaining things like major transitions in individuality, which involve changes in development and inheritance.

As Griesemer (2006) writes, “Because the origin of new levels involves the evolution of new developmental processes and not only the evolution of adaptations, there can be no escaping the need for an account of how heredity and development intertwine to co-produce conditions for evolvability” (p. 344).

Hull’s (1980) “replicator–interactor” framework was designed as an improvement over Lewontin’s (1970) levels of selection framework that would distinguish the units of variation or heredity from units of selection. The replicator–interactor distinction is a hierarchical generalization of Dawkins’s (1978) “replicator–vehicle” distinction, in which replicators and interactors can potentially be found at many levels of organization as long as entities at that level fulfill the requisite functional role. A replicator is any entity that passes on its structure through direct replication or copying. An interactor is any entity that “directly interacts as a cohesive whole with its environment in such a way that replication is differential” (Hull, 1980, p. 318). Although the replicator–interactor framework purports to provide a decomposition of levels under the evolutionary process (Hull, 1980, pp. 312–313), this decomposition is defective for two reasons.¹¹

First, it abstracts only outcome-based definitions from causal processes (Griesemer, 2006). In the case of replication, the outcome is structural similarity between original and copy, while material processes of inheritance are backgrounded (Griesemer, 2006). In the case of interactors, the outcome is differential replication, while ecological processes are backgrounded. This first defect leads right back to the same limitations of levels of selection just described. The second defect is that the replicator–interactor framework includes only two narrow subprocesses out of the wider process of developmental evolution—namely, inheritance and selection. This leads to a severely impoverished picture of evolution. By excluding development and its subprocesses, we lose any chance of capturing the causal structures that link genetic inheritance and selection. Moreover, by excluding development, the framework *cannot* incorporate insights about the hierarchical structure of variation, including features like network-level causation, variational independence above the genetic level, and shifting causality horizons in evolution.

6.6 Conclusion

The notion of levels of organization has multiple cross-cutting roles in the life sciences. Even when we restrict the discussion to only the most major of these roles (R1) to (R3), it is often difficult to actually identify compositional types (R1) that track causal structures (R2) that hold with generality (R3). I attributed this difficulty to the dissociability of structure and function in complex evolved systems. A consequence of this dissociability is that, as long as we wish to satisfy all three roles at once, it will be necessary to find some way of bridging structural and functional perspectives on levels. One way is to combine perspectives while relying on a characterizational or “cluster” approach to level placements, as I interpret Wimsatt (1976, 2007). Another way is to distinguish perspectives in terms of the causal processes they track and decompose levels under a single unified causal process. In the process-relative approach, placement at levels is based on constitution relationships between causal processes. This has the effect of restricting the structures or components to those that participate in the focal process, thereby making level placements less ambiguous, while also including dynamical categories in the range of generalizations about levels (R3). These two

approaches are complementary and opt for different trade-offs between generality and specificity. The general picture can be reached from the process-relative approach by aggregating multiple perspectives and identifying levels where there are robust points of convergence between them (see Wimsatt, this volume; Griesemer, this volume).

The roles for levels start to acquire more concrete significance when we descend from the thin air of metaphysics of science to an empirical context. The case study investigated in section 6.5—decomposition under the process of developmental evolution—yields a hierarchy concept with several distinctive features. Not all parts and processes of organisms are placed into levels (R1), and those that are possess the special property of variational independence (R2) in either the entity or process at a given level. Variational independence can ground the notion of a “causality horizon” in comparative evo-devo, which marks the limits of reduction as well as privileged levels of generalization (R3). The end result is an evolutionary picture of levels that is deeper than the effect-functional frameworks of levels of selection and replicator–interactor levels, while also including them as partial subprocesses of developmental evolution.

The approach proposed here is not a complete framework for thinking about levels in evolutionary and developmental biology, but it is hoped that this initial attempt can open up a more expansive role for levels in future theorizing. One future direction will be to integrate metabolic or physiological perspectives on development. A key insight of Waddington’s three-process hierarchy of evolution–development–metabolism was that any theory that does not include all three is destined to be incomplete in some crucial respect (Waddington, 1957, p. 6). Work in evo-devo often operates with the narrow understanding of development as the acquisition of specific regulatory states in cell populations, which is explained in terms of modular gene networks. In the background are more systemic, nonmodularized metabolic processes such as growth, resource competition, tissue-level mechanics and regulation, and character–character interaction generally. Integration of these processes within a broader conception of development might show that modularity of gene networks does not translate to modularity at higher levels of development (Gawne et al., 2020; Nijhout & Emlen, 1998). A second future direction will be to move from descriptions of variational independence across levels to explanations of its occurrence (DiFrisco, forthcoming; DiFrisco et al., 2020). This might follow general explanations deriving from the tradition of Simon (1962) and Wimsatt (1976, 2007) of why there are levels of organization at all, but contextualized specifically to the process of evolution.

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Notes

1. Note that Craver (2015, 19n22) neither endorses nor rejects token identity across levels, although he does recognize the descriptive feature of “part loss” when we ascend to higher levels. See section 4 for further details.
2. The same point has also been made by Alan Love and Bill Wimsatt.

3. Thanks to Jim Griesemer for prompting this idea.
4. See also Griesemer (2018) for a complementary exploration of the idea of “process-relativity of individuation” or “process realism with entity relativism” in the context of biological individuality.
5. The causal nature of processes could also be explicated in terms of our ability to *manipulate* it at one time and observe changes in the process at a later time.
6. Amundson (2005) calls this the “causal completeness principle” (p. 176).
7. At this point, the question arises whether descriptive complexity and perspectival pluralism re-enter the process-relative levels but at a finer grain than with general levels of organization. This seems to some extent unavoidable, but the goal is to reduce ambiguity rather than eliminate it entirely. The structure of perspectives-within-perspectives nonetheless does not seem to be genuinely fractal or iterated at all scales of conceptual resolution.
8. Those promoting *eco-evo-devo* can be interpreted as advocating for either the inclusion of more ecological variables into the study of developmental evolution or, more radically, the inclusion of ecological parts and processes within the boundaries of an “extended development” (Gilbert & Epel, 2009; see Griesemer, 2019, this volume). In this chapter, I wish to use the term “development” in a way that is compatible with both extended and restricted views of organism boundaries.
9. Note that the notion of a “character” is not used here in the wide sense from systematics of any “characteristic,” which would apply to all lower levels as well. “Characters” in the narrow sense are body parts or gross phenotypic features, and there are often hierarchical relationships within a single character complex (e.g., digits as part of the autopod or vertebrae as parts of the vertebral column).
10. Note that variational independence across levels is neither randomly nor uniformly distributed, and the conserved correspondences possess special significance for a mechanistic theory of character identity. See DiFrisco et al. (2020).
11. The same criticism applies to more recent frameworks based on the distinction between “genealogical” and “economic” hierarchies, which is a hierarchical generalization of the replicator–interactor distinction.

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